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Tables, one to a page, should be double-spaced throughout and be assigned consecutive Arabic numerals. Collect all figure legends on a separate page. Each illustration should be centered on a single page and be no smaller than final size and no larger than twice final size. The name of the author(s) and figure number, assigned consecutively using Arabic numerals, should be pencilled on the back of each figure.

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COVER: Adult female Barred Forest-Falcon (*Micrastur Ruficollis*) with female Dot-winged Antwren (*Microrhophias Quixensis*). Painting by N. John Schmitt.

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DIFFERENTIAL WINTER DISTRIBUTION OF ROUGH-LEGGED HAWKS (*BUTEO LAGOPUS*) BY SEX IN WESTERN NORTH AMERICA

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ABSTRACT.—We conducted roadside surveys of Rough-legged Hawks (*Buteo lagopus*) in Montana, California, and Nevada for four consecutive winters from 1995–96 through 1998–99. The proportion of adult males to adult females and of adults to juveniles in the samples did not change significantly throughout the winter at any location. Adult females outnumbered adult males on all but one survey in Montana, and adult males outnumbered adult females on every survey in California and Nevada. The mean ratio of males to females was significantly lower in Montana than in the southerly locations, suggesting that on average, females wintered farther north than males. Furthermore, the annual mean percentage of adult females at all locations was correlated with average temperature and snowfall. The ratio of adults to juveniles did not differ significantly between locations within a year, suggesting there was no differential winter distribution by age. However, the proportion of juveniles in each location varied significantly among years. The sex ratio of juvenile Rough-legged Hawks trapped in Montana was nearly identical to ratios observed for adults on road surveys. Sex ratios of 63 museum specimens provided further evidence that, on average, female adult and juvenile Rough-legged Hawks winter farther north than do males. We reviewed three hypotheses for latitudinal segregation of the sexes and suggest that thermal regulation is an important factor influencing differential winter distribution in Rough-legged Hawks.

KEY WORDS: *Buteo lagopus*; *Rough-legged Hawk*; *roadside raptor surveys*; *winter distribution*; *latitudinal segregation*; *differential migration*.

Distribución diferencial por sexo de *Buteo lagopus* al pasar el invierno en el oeste de Norteamérica

RESUMEN.—Llevamos a cabo conteos de carretera de *Buteo lagopus* en Montana, California, y Nevada por cuatro inviernos consecutivos desde 1995–96 hasta 1998–99. La proporción de machos adultos en relación a hembras adultas y de adultos a juveniles en la muestra no varió significativamente a través del invierno en ninguna localidad. Las hembras adultas sobrepasaron a los machos adultos en todas las localidades exceptuando a Montana y los machos adultos sobrepasaron a las hembras adultas en cada monitoreo en California y Nevada. La proporción media de machos a hembras fue significativamente más baja en Montana que en las localidades del sur, lo que sugiere que en promedio, las hembras pasaron el invierno más al norte que los machos. Aún más, el porcentaje de la media anual de hembras adultas en todas las localidades fue correlacionado con la temperatura promedio y la precipitación de la nieve. La proporción de adultos y juveniles no difirió significativamente entre localidades entre años, lo cual sugiere que no existió una diferencia por edades de la distribución de individuos que pasan el invierno en este sitio. Sin embargo, la proporción de juveniles en cada localidad varió significativamente entre años. La proporción de sexos de 63 especímenes de museo provee evidencias de que en promedio las hembras adultas y los juveniles de *Buteo lagopus* pasan el invierno más al norte que los machos. Resumimos tres hipótesis para la segregación latitudinal por sexos y sugerimos que la regulación térmica es un factor importante que influye en la distribución diferenciada de *Buteo lagopus*.

[Traducción de César Márquez]

Rough-legged Hawks (*Buteo lagopus*) are Holarctic raptors that, in the western United States and Canada, winter from southern British Columbia and Alberta, south through California and New Mexico (American Ornithologists' Union 1998). As do all North American buteos, they exhibit reversed sexual size dimorphism, with females being larger than males. Several studies have provided evidence of differential winter distribution (Russell 1981, Kjellén 1994). Kjellén (1994) studied migrant and wintering Rough-legged Hawks in Sweden and found significantly more adult females and juveniles among wintering birds than among southbound migrants in autumn, although this was not consistent for every year of the study. Russell (1981) examined Rough-legged Hawk specimens collected from mid-December–mid-February in the eastern United States and found that females predominated in the north and males were more numerous in the southern portion of the range. However, he did not determine the age of specimens. Contrary to Kjellén (1994), Mindell in Palmer (1988) reported that juvenile Rough-legged Hawks tend to migrate farther south than adults in North America.

Several hypotheses have been proposed to explain differences in winter distribution between sex and age classes in birds. The arrival-time hypothesis suggests that the sex which establishes the territory (usually males) should winter closest to the breeding grounds (King et al. 1965, Myers 1981, Wallin et al. 1985, Kjellén 1994). The social-dominance hypothesis proposes that subordinates which cannot compete successfully for resources with dominant birds migrate farther south or use suboptimal habitats (Gauthreaux 1985, Kerlinger and Lein 1986). The body-size hypothesis asserts that because of thermal advantages, larger individuals winter farther north than smaller individuals (Ketterson and Nolan 1976, Searcy 1980).

The purpose of our study was to determine the age and sex ratios of Rough-legged Hawks wintering in western North America within, between, and among winters to better understand their winter distribution. Furthermore, we wanted to explore the possible causal effects of the observed sex and age distributions.

STUDY AREAS AND METHODS

This study was conducted in the Mission Valley, Montana (47°50'N, 114°25'W), Sierra Valley, California (39°60'N, 120°25'W), and Lovelock Valley, Nevada (40°25'N, 118°50'W) (Fig. 1). Study sites were chosen be-

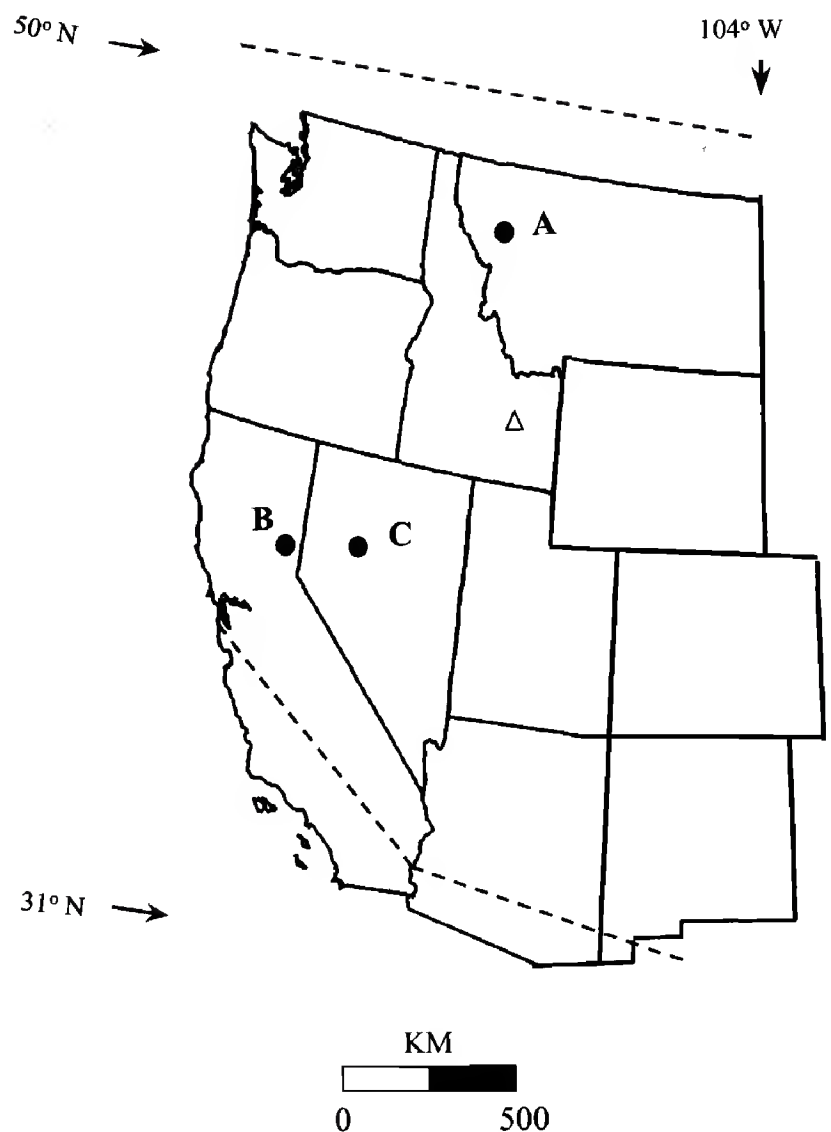


Figure 1. Mission Valley, Montana (A), Sierra Valley, California (B), and the Lovelock Valley, Nevada (C) study sites in the western United States. Also shown is Watson's (1984) study site in Idaho (open triangle) and approximate northern and southern extent of Rough-legged Hawk wintering range (shown by dashed line; Palmer 1988).

cause of their abundance of wintering raptors. The Mission Valley is in the northern portion of the winter range of the Rough-legged Hawk. Land use in these areas is predominately agriculture and livestock grazing. The Sierra and Lovelock valleys are 1130 km and 960 km farther southwest, respectively, in the mid to southern portion of the Rough-legged Hawk's winter range (see Palmer 1988). Each of these valleys has an extensive system of secondary roads with limited vehicular traffic and numerous utility poles and fence posts that are used by perching hawks.

The Mission Valley (40 × 20 km) is in west-central Montana approximately 65 km north of Missoula at an elevation of about 800 m. The Sierra Valley (30 × 15 km) is in the Sierra Nevada Mountains, California, approximately 40 km northwest of Reno, Nevada, at an elevation of about 1500 m. The Lovelock Valley (30 × 20 km) is 145 km northeast of Reno, Nevada, at an elevation of approximately 1200 m.

We conducted 27 roadside surveys from November through April during four consecutive winters from 1995–99, hereafter referred to as winters one through

four. Of these, 21 were conducted in Montana (i.e., northern location), and 6 in California and Nevada (i.e., southern locations). One transect was surveyed monthly in the Mission Valley during each winter except the first, during which two transects were surveyed simultaneously (by two groups of observers). The survey day varied among winters one through four; surveys were conducted near the beginning of the month during winters one and two, and on day 20 of each month during winters three and four. The two transects in the Mission Valley were 63 and 60 km long, respectively. The 60-km transect was abandoned after the first winter, and the longer transect was reduced to the last 43.5 km after the first survey of the second winter because of time restrictions. Thereafter, the 43.5-km transect was surveyed consistently. One 73-km transect was surveyed monthly in the Sierra Valley the second winter, and opportunistically the third and fourth winters. Finally, one 48-km transect was surveyed in the Lovelock Valley, Nevada, during the first and second winters (both in January).

Surveys began between 0830–1030 H, depending on the time of year, to allow enough time for hawks to disperse from roost sites to foraging areas. Each transect was surveyed by two observers in one vehicle traveling at a continuous speed of 25–35 kph and took 2.5–4.5 hr to complete depending on the number of birds sighted. Observers stopped the car to determine the age and sex of each bird sighted. All birds were initially detected without the use of optics, after which binoculars and 15–45 \times spotting scopes were used for species identification and determination of age and sex. The sex, age, activity, distance from observer, location, and time were recorded for every Rough-legged Hawk sighted. Multiple features were used for determining sex and age based on Cade (1955), Clark and Wheeler (1987) and Wheeler and Clark (1995). Juvenile Rough-legged Hawks cannot be sexed by plumage, so sex determination was confined to adults. Any uncertainty in the identification of sex or age was recorded as “unknown.”

In addition to doing road surveys, we also obtained the sex ratios of Rough-legged Hawks collected throughout the western U.S. (west of 104°W) from various museums (see acknowledgments for list of museums). We limited the analysis to specimens collected between 1 December–28 February to minimize the number of migrating birds in the sample. To examine whether a latitudinal gradient existed, we divided the specimens into three latitudinal ranges: 31°–40°, 41°–46° and 47°–49°N.

For assessing the sex ratio of juvenile Rough-legged Hawks, we inspected trapping data from Montana. As part of a separate study, Rough-legged Hawks were trapped, banded, and radiotagged each winter in Montana since 1995. The age and sex of each hawk was determined using plumage characteristics, iris color, and body measurements. Also, for investigating social interactions, we conducted extensive behavioral observations on radio-tagged birds in Montana, recording all intraspecific and interspecific interactions. All interactions involving noninstrumented birds were also recorded. A bird was described as “winning” an interaction if it: (1) successfully displaced another bird from a perch or from the immediate “air space” (Bildstein 1987) or (2) successfully defended a perch or “air space” when chal-

lenged by another bird. Thus, the frequency of “winning” interactions considered both the instigator and the recipient.

We used a chi-square test to evaluate differences between sex and age ratios throughout each winter at a location. Because survey data were analyzed as proportions, they were arcsine transformed (Wilkinson et al. 1996). Differences in sex and age ratios between and among years and among locations were tested with ANOVA and Tukey’s pairwise comparisons using SYSTAT 7.0 (Wilkinson et al. 1996). The survey conducted the first winter was not included in the statistical analysis because it was the only survey done in a southern location that year. Additionally, because survey results from California and Nevada were nearly identical, they were combined and are heretofore referred to as southern surveys. Five surveys were excluded from the analysis because fewer than seven hawks were detected. Two other surveys attempted in California were abandoned because of poor visibility, and two surveys were not included in the analysis of age ratio because they were diagnosed as outliers.

Climatological data for the Mission Valley were obtained from the Western Regional Climate Center. We tested for correlations between sex ratio and climatic differences between and among years using the Pearson correlation. We did not compare climatological data with the southern locations because of the lower number of surveys and inconsistency of survey dates. A one-sided Mann-Whitney *U* procedure was used for testing whether female specimens were recovered farther north than males for the museum specimens. Finally, data were checked for skewness, normality, outliers, homogeneity of variances, and auto-correlation (Wilkinson et al. 1996).

RESULTS

We detected more adult males than females on all surveys in the southern locations, and more adult females than males on all surveys in the northern location, except for one in February of the third winter (Table 1). The proportion of adult males to adult females did not vary significantly throughout a winter in any location (Chi-square test; $P > 0.05$); however, the sex ratio was significantly different between the northern and southern locations within and among winters (Table 2). The proportion of females detected on surveys in the northern location was significantly lower in the third winter compared with the first but did not differ significantly between any consecutive winters (Table 2). However, the mean percentage of adult females was significantly inversely correlated with average temperature ($r = -0.982$, $df = 3$, $P = 0.018$) and less strongly correlated with average snowfall ($r = 0.901$, $df = 3$, $P = 0.099$) among winters in Montana.

The proportion of adults to juveniles did not vary significantly within any winter in any location (Chi-square test; $P > 0.05$) (Table 3); however, the

Table 1. Percentage of adult female Rough-legged Hawks (number of adults in parentheses) detected on surveys in northern (N = Montana) and southern (S = Nevada and California) locations during four consecutive winters (1–4) from 1995–96 through 1998–99. Climatic data shown at the bottom of the table include the average deviation from monthly normal, averaged for each winter.

MONTH	MONTANA				CALIFORNIA			
	N1	N2	N3	N4	S1	S2	S3	S4
Nov.	69 (13)	62 (29)	57 (14)	70 (46)		20 (5)	33 (9)	33 (3) ^a
Dec.	80 (10)		65 (26)	60 (42)		29 (7)		
Jan.	79 (19)	77 (13)	61 (31)	55 (56)	11 (9) ^b	20 (5)		0 (1) ^a
Feb.	77 (22)		49 (35)	63 (35)		33 (12)		
Mar.	73 (11)	75 (12)	67 (33)	74 (39)		0 (2) ^a	29 (7)	
Apr.	71 (7)	73 (22)	100 (1) ^a	67 (6)		100 (1) ^a		
Mean % ± SD	75 ± 4	72 ± 7	60 ± 7	65 ± 5	11 ± 0	27 ± 7	31 ± 3	
Ave. temp (C°) ^c	−0.86°	−0.51°	+2.8°	+3.1°				
Snowfall (cm) ^c	+3.6	+9.4	−14.3	−6.3				

^a Survey not included in analysis because fewer than 7 hawks were detected.
^b Survey not included in analysis because it was the only one done in a southerly location the first year.
^c Average monthly deviation from 90-year climate averages, Nov.–Feb., recorded at St. Ignatius, Montana by the Western Regional Climate Center.

age ratio differed significantly between and among most winters in each location (Table 4). Still, the age ratio was not significantly different between northern and southern locations within a winter (Table 4). Additionally, the average percentage of adults among winters in Montana was not correlated with differences in average temperature ($P =$

Table 2. Pair-wise mean comparison (ANOVA, Tukey's method) of sex ratio between northern (N) and southern (S) locations in winters 1–4 (1995–99). Sex ratios of male and female Rough-legged Hawks differed significantly between northern and southern locations both within and among winters.

	N1	N2	N3	N4	S2	S3
N1	1.00					
N2	0.97	1.00				
N3	0.01*	0.10	1.00			
N4	0.11	0.55	0.79	1.00		
S2	0.00**	0.00**	0.00**	0.00**	1.0	
S3	0.00**	0.00**	0.00**	0.00**	0.9	1.0

* Significant at 0.05 alpha level.
** Significant at 0.001 alpha level.

0.89) or snowfall ($P = 0.53$). Finally, the number of Rough-legged Hawks (birds/km) differed greatly between the first winter and all remaining winters in Montana, but numbers fluctuated considerably less among years in California (Table 3).
The proportion of hawks per survey where the age, sex, or both, were unknown averaged $12\% \pm 1$ (± 1 SE, range = 0–35%). We had a lower number of unknown hawks on surveys that recorded the greatest number of individuals, as well as on sunny days when hawks tended to soar in thermals.
Of the 65 museum specimens examined, we found that females were recovered significantly farther north on average than males (one-sided Mann-Whitney U , $P = 0.019$, ages not distinguished, Table 5). Furthermore, the sex ratios were similar to those recorded on road surveys at equivalent latitudes. The three lowest latitude specimens were males (min $\approx 31^\circ$; a juvenile male collected near El Paso, Texas), and the four specimens collected from the highest latitude ($\geq 48^\circ$) were all females. Additionally, the mean latitude for male and female specimens was $43^\circ \text{ N} \pm 4.2$ and $45^\circ \text{ N} \pm 2.8$, respectively.

Table 3. Percentage of adult Rough-legged Hawks (number of hawks in parentheses) detected on surveys in northern (N = Montana), and southern (S = Nevada and California) locations during four consecutive winters (1–4) from 1995–96 through 1998–99. Also, average number of Rough-legged Hawks/km (i.e., hawk density) on survey route for November–February surveys each winter.

MONTH	MONTANA				CALIFORNIA			
	N1 ^a	N2	N3	N4	S1	S2	S3	S4
Nov.	100 (13)	62 (47)	74 (19)	87 (53)		63 (8)	82 (11)	50 (6) ^b
Dec.	100 (10)		81 (32)	78 (54)		58 (12)		
Jan.	86 (22)	45 (29)	79 (39)	78 (72)	75 (12) ^c	71 (7)		100 (1) ^b
Feb.	92 (24)		83 (42)	70 (50)		60 (20)		
Mar.	65 (17) ^d	50 (24)	89 (37)	80 (54)		67 (3) ^b	88 (8)	
Apr.	87 (8)	69 (32)	33 (3) ^b	40 (15) ^d		100 (1) ^b		
Mean % ± SD	88 ± 13	56 ± 11	81 ± 6	72 ± 16	75	63 ± 6	85 ± 4	75
RLHAs/km	0.33	1.1	0.86	1.4	0.25	0.16	0.15	0.05

^a Sum of two transects.
^b Survey not included in analysis because of the low number of hawks detected.
^c Survey not included in analysis because it was the only one done in a southerly location the first year.
^d Survey not included in analysis because it was diagnosed as an outlier.

We trapped 55 Rough-legged Hawks in Montana from 1995–99 (20 adults and 35 juveniles). Overall, 55% of adults and 77% of juveniles were female, based on measurements (Table 6). The number of juvenile females trapped outnumbered juvenile males every year; however, adult females only outnumbered adult males in the third and fourth winters (Table 6). For juveniles, the average propor-

tion that was female was 76.6% and ranged among winters from 83.3% (1995–96) to 66.7% (1998–99). We recorded 171 intraspecific and 85 interspecific interactions while tracking and observing 17 (7 adults, 10 juveniles) instrumented hawks during the winters of 1997–98 and 1998–99. Thirteen percent of 123 intraspecific interactions between known-age birds involved adult females displacing adult males, compared with <1% where adult males displaced adult females (Table 7). However, interactions between and within other age and sex

Table 4. Pair-wise mean comparisons (ANOVA, Tukey’s method) of age ratio between northern (N) and southern (S) locations in winters 1–4 (1995–99). Age ratio differed significantly between northern and southern locations between and among most winters, but were not significantly different within a winter (shown in bold).

	N1	N2	N3	N4	S2	S3
N1	1.00					
N2	0.00**	1.00				
N3	0.08	0.01*	1.00			
N4	0.03*	0.01*	0.99	1.00		
S2	0.00**	0.95	0.03*	0.08	1.00	
S3	0.34	0.02*	1.00	0.99	0.10	1.00

* Significant at 0.05 alpha level.
** Significant at 0.001 alpha level.

Table 5. Sex composition of Rough-legged Hawk specimens collected from different latitudes between 1 December–28 February, and west of 104°W longitude in the western United States (see Acknowledgments for list of museums).

LATITUDE (°N)	N	% FEMALES
47°–49°	25	68 (17)
41°–46°	24	62 (15)
31°–40°	16	31 (5)

Table 6. Age and sex composition of Rough-legged Hawks trapped in the Mission Valley, Montana (Olson unpubl. data).

YEAR	SEX RATIO (M:F)	
	ADULT	JUVENILE
1995–96	4:1	1:5
1996–97	2:1	3:11
1997–98	2:4	2:7
1998–99	1:5	2:4
Total: M	9 (45%)	8 (23%)
F	11 (55%)	27 (77%)

classes occurred more frequently. Juveniles failed when attempting to displace adult females and adult males 45% and 25% of the time, respectively, whereas adults rarely failed when attempting to displace juveniles (Table 7). When comparing the ratio of aggressive encounters won versus the total number of aggressive encounters for each age and sex class, we found adult females won 85% ($N = 108$) of interactions, compared with 42% for adult males ($N = 33$), 72% for juvenile females ($N = 46$) and 33% for juvenile males ($N = 15$). The mean occurrence-rate of aggressive intraspecific interactions was 0.387/hr ($N = 17$) over 384 total hours of observation.

DISCUSSION

Our observations indicated that adult female Rough-legged Hawks tend to winter farther north than adult males, but that differential migration does not occur between adults and juveniles. Watson (1984) reported that 81% of all Rough-legged Hawks were adults and 69% of adults were males in his study site in southern Idaho (43°45'N, 112°45'W), which lies midway in latitude between our northern and southern study sites (Fig. 1). Watson's ratio of adult males to adult females was larger than that in Montana and smaller than that in California and Nevada, suggesting a latitudinal gradient in the distribution of the sexes. Additionally, Russell (1981) examined 42 male and 64 female specimens (adults and juveniles) collected between 10 December–14 February in the eastern United States (east of 104°W) and found that females wintered, on average, 3° farther north than males. Furthermore, Russell showed a clear gradient in sex ratio from north to south. When we combined this evidence with the sex ratios record-

Table 7. Frequency of intraspecific perch displacement between and among different age and sex classes of Rough-legged Hawks wintering in the Mission Valley, Montana, 1997–99. Failed displacement attempts are shown in parentheses. Interactions involving one or both birds of unknown age and sex are excluded.

DISPLACER–DISPLACED	FREQUEN- CY	RELA- TIVE	
		FRE- QUENCY	% FAILED
Adult female–Juv (unk sex)	39 (1)	32%	3%
Juv (unk sex)–Juv (unk sex)	25 (5)	20%	17%
Adult female–Adult female	23 (1)	19%	4%
Adult female–Adult male	16	13%	0%
Adult male–Juv (unk sex)	6	5%	0%
Juv (unk sex)–Adult female	6 (5)	5%	46%
Adult male–Adult male	4 (1)	3%	20%
Juv (unk sex)–Adult male	3 (1)	2%	25%
Adult male–Adult female	1	1%	—
Total	123 (14)	—	—

ed for museum specimens in the western United States, a gradient from north to south, with predominantly females in the north and males in the south, appeared to be consistent (Table 5). Although certain biases can be introduced by using museum collections, the sex ratios were similar to those observed on road surveys at the same latitudes.

Because Russell (1981) did not distinguish adults from juveniles, it has remained largely unknown whether juveniles also exhibit differential migration between the sexes. Seventy-seven percent of juveniles trapped in the Mission Valley, Montana, during the winters of 1995–99 were females based on measurements. Moreover, the highest proportion of juvenile females occurred the same year that we observed the highest proportion of adult females on road surveys and the lowest densities of hawks. Differential trapability between sexes could bias the sex ratio of trapped birds; indeed, adult females tended to be more difficult to trap than adult males. However, if this pattern were true for juveniles, then the trapping ratios would underestimate rather than overestimate the proportion of juvenile females. Furthermore, juveniles are much more easily trapped than adults, and the likelihood of juvenile males being so consistently underrepresented seems small. Therefore, we concluded that the trapping data indicated that sex differenc-

es in winter distributions are similar for adults and juveniles.

Intraspecific interactions and territoriality in Rough-legged Hawks during winter are highly complex and poorly understood (Watson 1984, Bildstein 1987, Palmer 1988). Aggression and territoriality may change daily depending on weather (Temeles and Wellicome 1992), food availability, and a variety of other unknown factors (Watson 1984). Watson recorded the frequency of aggressive intraspecific interactions between known-sex Rough-legged Hawks wintering in Idaho and found that 70% of all interactions ($N = 76$) involved females displacing males. Watson (1984) did not distinguish between juveniles and adults, however. When separating the different age and sex classes, we found that adult females displaced adult males much more frequently. Additionally, adult females displaced other adult females more often than adult females displaced adult males, which differed greatly from Watson's (1984) findings in Idaho. When considering the success rate of displacement attempts and the overall success rate for each age and sex class, it appeared that adult females are the most dominant class and juvenile males are the least dominant. Interactions between adult males and juvenile females were more complicated and remain poorly understood. Two major differences between Watson's (1984) study site and the Montana study area, were that Rough-legged Hawks in Idaho frequently fed on road-killed carrion, whereas hawks in the Mission Valley rarely fed on carrion and foraged almost exclusively on small mammals (C. Olson unpubl. data) and the densities of Rough-legged Hawks were much higher in three of four years in the Mission Valley ($\bar{x} = 1.14$ birds/km) than in Idaho ($\bar{x} = 0.18$ birds/km; Watson 1984). It is unknown, however, how these factors influence the social interactions of Rough-legged Hawks during winter.

The ratio of juveniles to adults on the road surveys did not differ significantly within a season; however, the proportion of juveniles did vary among winters. Furthermore, the overall density of Rough-legged Hawks in Montana was considerably lower in the first winter than in the following three winters. The low numbers observed in the first winter followed a major decline in voles (*Microtus* spp.) in the area. Rough-legged Hawk numbers are known to fluctuate considerably (Baker and Brooks 1981, Mindell and White 1987, Palmer 1988, Virkkala 1992, Swem 1996, Potapov 1997),

and fluctuations in the number of wintering juveniles are often attributed to changes in reproductive success prior to the subsequent winter (Bent 1937, Brown and Amadon 1968). However, a variety of local and regional factors such as prey availability, weather, and/or the presence of conspecifics, also may influence the distribution and density of wintering juveniles.

REVIEW OF HYPOTHESES

Based on the arrival-time hypothesis, we would expect the sex that establishes the breeding territory to winter farthest north. Several lines of evidence suggest that the arrival-time hypothesis does not apply to Rough-legged Hawks. First, males usually establish territories in most North American raptor species (Newton 1979, Johnsgard 1990), and hence we would expect to find a preponderance of adult males wintering farther north. Second, although not well-documented, Rough-legged Hawks are thought to arrive on the breeding grounds already paired (Bent 1937, Mindell and Palmer 1988). If pairs do arrive simultaneously, such behavior would be inconsistent with the arrival-time hypothesis. Finally, the arrival-time hypothesis would act predominately on breeding birds (Myers 1981), and because juvenile Rough-legged Hawks are not likely to breed in their first season, we would not expect similar latitudinal segregation among juveniles (Kjellén 1994).

The social-dominance hypothesis proposes that subordinate individuals are forced to winter farther south to avoid competition with dominant conspecifics (Gauthreaux 1985). Hence, the dominant sex would be expected to display aggressive behavior toward individuals of the opposite sex and/or subordinate age classes, especially in more northern wintering areas. In Rough-legged Hawks, the larger females should be dominant within each age class. Thus, according to the social-dominance hypothesis, adult females should winter farthest north, juvenile males farthest south, and adult males and juvenile females overlapping in the middle, depending on which class is most dominant (Kerlinger and Lein 1986).

Although it appears that adult female Rough-legged Hawks are dominant over the other classes, and juvenile males tend to be subordinate, it remains unclear whether juvenile females dominate adult males, or vice versa. Roughly 70% of behavioral interactions did not involve adult males. Conversely, 64% of interactions involved juveniles, sug-

gesting that frequency of antagonistic interactions, alone, does not explain why Rough-legged Hawks exhibit differential migration by sex and not age. Although habitat segregation by sex has been attributed to social dominance in other species (Koplin 1973, Mills 1976), studies supporting the social-dominance hypothesis have failed to show that intraspecific competition, and not various environmental factors, results in the latitudinal segregation of the sexes.

If our data accurately reflect the sex ratios of juvenile hawks wintering in the Mission Valley, then they indicate that similar selection pressures are acting equally on adults and juveniles. If social dominance were the main operating factor, we would expect juvenile males to occur in lower proportions than adult males in the more northern areas. Furthermore, the sex ratio of adults should change as food availability decreases and/or as hawk densities change, as would be expected by the social-dominance hypothesis. However, the sex ratios changed very little between years of extremely low densities and presumably limited food (1995–96 pers. obs.), and extremely high wintering densities with abundant food (1998–99 pers. obs.) in Montana. Indeed, although Russell (1981) favored the social-dominance hypothesis for explaining differential migration by sex in Rough-legged Hawks, he suggested that the migration patterns may be flexible, varying as regional environmental conditions vary.

We propose that the most influential factor regulating differential winter distribution in the Rough-legged Hawk is thermoregulation and tolerance of more extreme winter conditions, i.e., the body-size hypothesis (Ketterson and Nolan 1976, Searcy 1980). In Montana, we detected the highest proportions of adult females on December and January surveys, and the highest proportions of adult males on the first and last surveys, during the two coldest winters (1995–96 and 1996–97). Moreover, the mean ratio of adult females to adult males in Montana was significantly inversely correlated with average temperature, and less-strongly correlated with average snowfall, among the four winters. Cade (1955) found no overlap in body mass between sexes of Rough-legged Hawks, although the sample sizes were small. When considering all morphological measurements, Cade and Palmer (1988) both estimated a minimum of 75% non-overlap between the sexes. So, female Rough-legged Hawks are clearly larger on average than

males. Herreid and Kessel (1967) determined for 31 species of birds that larger individuals have relatively heavier plumage and more effective insulation than smaller birds. Finally, Root (1988) suggested that larger body size increases potential energy stores and therefore enables longer periods of fasting, and further claimed that energy constraints eventually limit the distribution and abundance of species. If this is true for Rough-legged Hawks, then females may be more capable than males of withstanding colder temperatures and fasting during periods of deep snow and low prey availability. Therefore, we believe thermoregulatory constraints may be an important factor contributing to the differential latitudinal winter distribution of the sexes in the Rough-legged Hawk. Because the predictions of the social-dominance hypothesis overlap with those of the body-size hypothesis, it is difficult to completely disprove one or the other hypothesis. Clearly, further research is needed on the differences between the sexes in thermal conductance and the behavioral differences among the ages and sexes in territoriality.

Other suggested possibilities explaining female hawks wintering farther north than males, include greater prey-switching capability, interspecific competition or both (T. Swem pers. comm.). Because females are larger overall, they should be more capable of switching to alternative prey-types during periods of deep snow and subsequently low prey availability. Rough-legged Hawks are recognized as small mammal specialists; however, a variety of small and medium birds have been recorded at nests (Swem 1996), and road-killed carrion was commonly fed upon in Idaho (Watson 1984). Although neither of these ideas was specifically examined in this study, Rough-legged Hawks were seen foraging almost exclusively on small mammals, even throughout periods of deep (>10 cm) snow cover (Olson unpubl. data). Additionally, interspecific competition involving prey was likely much less than observed with hawks feeding on carrion in Idaho, because of the smaller size, faster consumption times and overall greater abundances usually associated with small mammals as prey. Therefore, these potential benefits for the larger sex may be in addition to, but probably are not, the actual operating factors.

Finally, we expected a greater proportion of males in Montana early and late in the season, especially during migration. Although we observed the highest proportion of males during November

and April, this was not significantly different from the rest of the winter. Russell (1981) also noted that sex ratios remained relatively unchanged during a winter. Thus, we suspect that migration, especially during fall, may be rapid and relatively continuous in birds wintering farther south, thereby explaining why we did not observe greater numbers of adult males stopping over in the Mission Valley during migration.

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AVAILABILITY AND INGESTION OF LEAD SHOTSHELL PELLETS BY MIGRANT BALD EAGLES IN SASKATCHEWAN

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ABSTRACT.—We determined food habits and prevalence of ingested shotshell pellets in a population of Bald Eagles (*Haliaeetus leucocephalus*) at a waterfowl staging area on the Canadian prairies. Food habits were ascertained through examination of prey remains and regurgitated castings, and by direct observation. Shotshell pellet ingestion was determined by radiography of regurgitated castings and by fluoroscopy of live-trapped eagles. In addition, we collected moribund and dead waterfowl to determine prevalence of lead shotshell pellets within their tissues. Waterfowl formed the bulk of the diet (>70% of prey items). Of 123 waterfowl carcasses examined, 47% contained shotshell pellets ranging in number from 1–7 per bird. Of 118 shotshell pellets removed, 87% were composed of lead, the remainder steel. Less than 2% of regurgitated eagle castings collected ($N = 509$) contained lead shotshell pellets. Ingested shotshell pellets were found in 9% (6 of 66) of trapped eagles. These conditions should ameliorate with the ban on use of lead shotshell pellets for hunting waterfowl in Canada that was instituted in 1999.

KEY WORDS: *Bald Eagle; Haliaeetus leucocephalus; food habits; lead shotshell pellets; lead exposure; Saskatchewan.*

Disponibilidad e ingestión de perdigones de plomo en águilas calvas migratorias en Saskatchewan

RESUMEN.—Determinamos los hábitos alimenticios y la prevalencia de perdigones ingeridos en una población de águilas calvas (*Haliaeetus leucocephalus*) en un área de aves acuáticas en las praderas de Canadá. Los hábitos alimenticios fueron evaluados a través del examen de restos de presas, egagrópilas y observación directa. La ingestión de perdigones fue determinada por radiografías de egagrópilas y por fluoroscopia de águilas atrapadas vivas. Adicionalmente, recolectamos aves acuáticas moribundas para determinar la prevalencia de perdigones de plomo dentro de sus tejidos. Las aves acuáticas conforman la mayoría de la dieta (>70% de las presas). De los 123 cadáveres de aves acuáticas examinadas, 47% contenían perdigones en un rango de 1–7 por ave. De los 118 perdigones removidos, 87% eran de plomo y el resto de acero. Menos del 2% de las egagrópilas recolectadas ($N = 509$) contenían perdigones de plomo. Los perdigones ingeridos fueron encontrados en el 9% (6 de 66) de las águilas atrapadas. Estas condiciones deben aminorarse con la prohibición del uso de perdigones de plomo en la caza de aves acuáticas en Canadá, instaurada en 1999.

[Traducción de César Márquez]

The presumed major source of lead for raptors is that obtained through ingestion of shotshell pel-

lets or bullet fragments present in tissues of prey animals (Redig et al. 1980, Pattee and Hennes 1983, U.S. Fish and Wildlife Service 1986, Gill and Langelier 1994). Bald Eagles (*Haliaeetus leucocephalus*) are particularly at risk to lead poisoning because they often rely on wounded prey or carrion likely to contain lead shotshell pellets (Pattee and Hennes 1983, Gerrard and Bortolotti 1988).

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Thus, lead toxicosis has been documented more frequently in Bald Eagles than in any other non-waterfowl species (Locke and Friend 1992).

In addition to unrecovered birds shot by hunters, free-flying waterfowl often harbor shotshell pellets embedded in body tissues (U.S. Fish and Wildlife Service 1986, Scheuhammer and Norris 1995). Wintering and migrant Bald Eagles frequently use locally abundant food sources such as waterfowl (Steenhof 1976, Sabine and Klimstra 1985, Hennes 1985, Lingle and Krapu 1986, Gerard and Bortolotti 1988). Thus, it is generally believed that the presence of waterfowl hunting and eagles in a localized area predetermine a high risk of lead poisoning for scavenging eagles (Pattee and Hennes 1983). In Canada, approximately 1500 metric tonnes of lead shotshell pellets are deposited annually into the environment by hunters shooting waterfowl, upland game birds and small mammals (Scheuhammer and Norris 1995).

Lead exposure and poisoning have been documented in both Bald and Golden Eagles (*Aquila chrysaetos*) from specimens collected on the Canadian prairies (Wayland and Bollinger 1999). Because of intense, localized waterfowl hunting in the southern portions of the Canadian prairies during the autumn and the concurrent passage of Bald Eagles with numerous waterfowl, eagles in this area have a high potential for lead exposure and poisoning. The purpose of this investigation was to determine the prevalence of lead shotshell pellets in potential prey items and to document the prevalence of ingestion of lead shotshell pellets by Bald Eagles at a waterfowl staging area under heavy hunting pressure.

STUDY AREA

We examined a congregation of Bald Eagles and waterfowl at Galloway Bay (50°48'N, 108°27'W), an impoundment located on the South Saskatchewan River in southwestern Saskatchewan, Canada. During the fall, in addition to attracting large numbers of Bald Eagles, the river and surrounding submerged floodplain together create favorable staging habitat for up to 700 000 geese and cranes (Roy 1996). The 10' block (10' latitude × 10' longitude) containing Galloway Bay is also among the most heavily used goose-hunting areas in Canada according to the Canadian Wildlife Service's National Harvest Survey (Canadian Wildlife Service unpubl. data).

METHODS

From September–November 1992–95, ancillary to trapping and blood sampling Bald Eagles to estimate lead exposure (Miller et al. in press), we collected data pertaining to food habits. We determined percent occur-

rence of food items using three techniques: analysis of regurgitated castings, collection of prey remains and direct observation. Each technique potentially under- or overrepresented certain prey items; therefore, we used all three methods simultaneously (Simmons et al. 1991, Mersmann et al. 1992).

Throughout the study area, whole or partially consumed carcasses were salvaged individually, while we compiled smaller items such as feathers or bones. The frequency of occurrence was determined for each species found in a particular day's collection. Prey remains not readily identified were compared with museum reference specimens (University of Saskatchewan and Royal Ontario Museum, Toronto, Ontario, Canada). Avian remains were identified to the lowest taxonomic category possible; all other remains were designated only to class.

Regurgitated castings were placed in separate bags and later fluoroscoped to determine prevalence of metallic shot. Castings were then air-dried at room temperature and examined under a dissecting microscope. A sample of approximately five similar feathers was examined under a compound microscope to determine downy bar-bule configuration as an aid in identification (Brom 1991) before using a reference collection or feather key (Broley 1950).

Under scientific and salvage permits acquired from Environment Canada, physically injured or moribund waterfowl were captured by hand and euthanized. Carcasses were frozen and later fluoroscoped in the laboratory to ascertain the presence of shotshell pellets. Shot-positive carcasses were radiographed frozen and left to thaw overnight. Shotshell pellets were excised and the tissue type and anatomical location from each embedded pellet or fragment noted. Lead and steel shotshell pellets were differentiated with a magnet.

We observed eagles hunting and eating. When possible, prey remains were retrieved after eagles had ceased feeding or after being flushed by an observer.

In 1994 and 1995, we used a Xi Scan 1000 Portable Radiographic and Fluoroscopic System (Xi Tech, Windsor Locks, CT U.S.A.) to examine the gastrointestinal tract of captured eagles to determine the prevalence of shotshell pellet ingestion (Miller et al. in press). Lead shotshell pellets could not be differentiated from steel or other nontoxic pellets, nor was the size of shotshell pellets determined.

Three eagles recaptured and fluoroscoped in the same season were included in analyses. Unlike blood lead (PbB) concentrations which may take several weeks to return to preexposure levels (Pain 1996), we considered initial and recapture dates independent, as shotshell pellets are likely not retained for long (Hoffman et al. 1981).

Unless indicated, nonparametric statistics were used throughout based on methods presented by Siegel and Castellan (1988). The Y-subscript following χ^2 tests indicates that a Yates' correction for continuity has been applied; the c-subscript following test statistics and z-values indicate that these values have been corrected for tied observations (Siegel and Castellan 1988).

RESULTS

Seventy-two collections were made during 1992–95. Avian remains were found in 97% of all collec-

Table 1. Comparison of prey identification techniques for Bald Eagles at Galloway Bay, Saskatchewan, 1992–95.

PREY	DIRECT OBSER- VATION ^a	PREY RE- MAINS ^{b,d}	CAST- INGS ^{c,d}
Unknown	22.8	—	—
Avian			
White-fronted Goose	28.1	66.7	49.0
Canada Goose	5.3	20.8	0.7
White Goose ^e	5.3	19.4	3.5
Anser spp.	7.0	22.2	5.6
American Coot	3.5	31.9	27.3
Mallard Duck ^f	3.5	19.4	13.3
Unidentified duck	3.5	13.9	27.3
Unidentified waterfowl	14.0	—	—
Mammals	1.8	8.3	8.4
Fish	5.3	9.7	2.8

^a % of all observations ($N = 57$).

^{b,c} % occurrence in all castings ($N = 143$) or collections ($N = 72$).

^d Does not total 100% as some items were found in occurrence with other items within the same casting or collection period.

^e Snow Geese (*Chen caerulescens*) and Ross' Geese (*C. rossii*).

^f *Anas platyrhynchos*.

tions (70 of 72), while mammals and fish were only found in six and seven (8 and 10%) collections, respectively (Table 1). White-fronted Geese (*Anser albifrons*) were the most common bird and were found in 48 of 72 (67%) collections; American Coots (*Fulica americana*) were the next most common avian prey and occurred in 32% of all collections (Table 1).

Of the 509 castings collected during 1994–95, 143 were examined to determine prey composition. Castings generally consisted of either one species or class (62%), although up to four species were identified in several pellets (3%). Of the three broad categories of prey items, fish and mammals were observed least often and were only found in 2.8% and 8.4% of castings, respectively (Table 1). Birds were the most common prey and were found in all regurgitated castings; six species and three genera were identified (Table 1).

Since observations of foraging eagles were generally made at a distance, assessing diet through feeding observations provided the least opportunity for identification of prey to the lowest taxon (Table 1). Seventy-five percent (43 of 57) of observations were of eagles eating; the remainder were of eagles hunting with no consumption of prey.

Birds accounted for at least 71% of all items that were consumed or actively pursued; fish and mammals combined accounted for only 7% of observations (Table 1).

Of note, however, was the response of eagles in 1995 to an avian cholera epizootic. Waterfowl mortality was noted on 22 October and we speculated that the outbreak began six days before on 16 October based on changes in the number of eagles that were observed feeding on the ground from population counts during the same period (Change-point test, $z = -3.62$, $P < 0.001$) (Miller 1999).

Of 123 fluoroscoped waterfowl carcasses of nine species, greater than 91% retrieved were geese; of these, 81% were White-fronted Geese (Table 2). Ducks, Sandhill Cranes (*Grus canadensis*) and American Coots accounted for only 9% of birds retrieved (Table 2). Ninety carcasses were dissected in the laboratory. The remaining 33 birds salvaged from the avian cholera epizootic in 1995 were fluoroscoped on site, and only the number of shotshell pellets present was recorded, as anatomical location could not be determined.

Significantly more birds with embedded shotshell pellets were obtained through sacrificing injured birds (40 of 68) than from specimens found dead through salvage (8 of 55) ($\chi^2_y = 23.226$, $P < 0.001$). Geese ($N = 112$) had a significantly larger median number of embedded shotshell pellets, or burdens, than an aggregate sample of ducks, Sandhill Cranes, and American Coots ($N = 11$) (Wilcoxon-Mann-Whitney, $z_c = -2.992$, $P = 0.0028$).

Embedded shotshell pellets were found in 40% of carcasses and in three of the nine species examined; among these three species, the median number of embedded shotshell pellets did not vary significantly (Table 2) (Kruskal-Wallis one-way ANOVA, $df = 2$, $H_c = 1.243$, $P = 0.54$). The number of pellets per carcass ranged from 1–7 (Table 2). We could not detect a difference in median shotshell pellet burden per anatomical region among carcasses with shotshell pellets (Kruskal-Wallis one-way ANOVA, $df = 2$, $P > 0.10$) (Table 2).

No evidence suggested a temporal increase in embedded shotshell pellet burdens in all species combined (Kendall's rank-order correlation, $T_c = 0.059$, $z_c = 0.961$, $N = 123$, $P = 0.34$). Neither did evidence support an increase among White-fronted Geese alone (Kendall's rank-order correlation, $T_c = -0.021$, $z_c = -0.294$, $N = 91$, $P = 0.39$) nor Canada Geese (*Branta canadensis*) (Kendall's rank-

Table 2. Summary of anatomical location and number of shotshell pellets excised from waterbirds at Galloway Bay, 1994–95.

SPECIES (N)	SHOTSHELL PRESENT?		PELLETS NO./ CARCASS	SUB- CUTAN. ^b	ANATOMICAL LOCATION OF SHOTSHELL PELLET ^a					
					BODY REGION					
	N	Y			GIZZARD	MUSCLE ^d	THOR. ^e	ABDOM. ^f	LEGS ^g	WINGS BONE ^h
White-fronted Goose (91)	52	39	1–7	21, 5	8, 0	20, 1	6, 0	8, 2	5, 1	25, 3
Canada Goose (14)	6	8	1–4	2, 0	0, 1	3, 0	3, 0	0, 2	2, 0	4, 1
Snow Goose (3) ⁱ	1	2	1–5	3	0	1	0	0	0	1
Ross' Goose (5) ^j	4	0	—	0	0	0	0	0	0	0
Sandhill Crane (1)	1	0	—	0	0	0	0	0	0	0
Mallard Duck (5)	5	0	—	0	0	0	0	0	0	0
American Coot (3)	3	0	—	0	0	0	0	0	0	0
Green-winged Teal ^k (1)	1	0	—	0	0	0	0	0	0	0
Northern Shoveler ^l (1)	1	0	—	0	0	0	0	0	0	0

^a The two numbers represent the number of shotshell pellets per location in birds that were collected live or found dead, respectively.
^b Shotshell pellets just beneath the skin.
^c Shotshell pellets within the lumen of the ventriculus or within the ventricular wall.
^d Shotshell pellets within muscle mass throughout the body excluding the legs and wings.
^e Shotshell pellets within the thoracic region.
^f Shotshell pellets within the abdominal region.
^g Shotshell pellets within muscle and bone of the legs.
^h Shotshell pellets within the bones and muscles of the wings and larger bones of the body were considered nonavailable to eagles.
ⁱ Birds were found dead.
^j One specimen was not fluoroscoped.
^k *Anas crecca*.
^l *Anas clypeata*.

order correlation, $T_c = 0.269$, $z_c = 1.339$, $N = 14$, $P = 0.090$).

Of all shotshell pellets excised ($N = 118$), 87.3% were composed of lead; the remainder were steel. Individual carcasses harbored either lead ($N = 40$), steel ($N = 2$) shotshell pellets, or both ($N = 6$). Lead shotshell pellets ranged in size from #6 to size BBB; steel shotshell pellets varied from #2 to size T.

During 1994–95, 509 castings were collected. All castings were fluoroscoped to determine if metallic shotshell pellets were present; 10 castings contained one metallic shotshell pellet of undetermined size. Four of 248 (1.6%) and four of 261 (1.5%) castings collected in 1994 and 1995 respectively, contained lead shotshell pellets, while the remaining two castings with shotshell pellets from 1995 contained steel shotshell pellets (2 of 261, or 0.8%). Contrary to our hypothesis, we did not detect an increase in the incidence of shotshell positive castings over the nine week period (16 September–16 November 1994–95) ($\chi^2 = 2.765$, $df = 3$, $P = 0.22$).

Intragastrintestinal shotshell pellets were observed in six of 69 eagles (8.7%). The 7.8% prev-

alence of lead exposure as determined from PbB concentrations (Miller et al. in press) was not significantly different from the exposure prevalence ascertained from ingestion of shotshell pellets ($\chi^2_y = 0.001$, $P = 0.96$). The number of ingested shotshell pellets per eagle ranged from 1–2. Four of the six eagles had shotshell pellets located in the abdomen, while the remaining two eagles each had single shotshell pellets present near the crop.

DISCUSSION

Waterfowl were the most common food of Bald Eagles at Galloway Bay. This dependence on waterfowl is typical for Bald Eagles wintering in the western United States (Steenhof 1976, Hennes 1985, Sabine and Klimstra 1985, Lingle and Krapu 1986). White-fronted Geese, the most abundant species at Galloway Bay, were also the most common species consumed. The second-most common prey items were ducks and American Coots, found in 41 and 27%, respectively, of all castings, and 32 and 39%, respectively, of all prey remains.

Occurring in <10% of prey remains, observations or castings, mammals and fish were uncom-

mon in the diet. However, we may have underestimated the proportion of each owing to differences in detectability (Frenzel and Anthony 1989, Mersmann et al. 1992, Watson et al. 1992).

The occurrence of shotshell pellets in 40% of debilitated or dead waterfowl at Galloway Bay is similar to the 20–30% reported for free-flying and apparently healthy waterfowl throughout the United States and Canada (U.S. Fish and Wildlife Service 1986, Scheuhammer and Norris 1995).

Waterfowl sampled late in or after the hunting season and individuals that have survived successive hunting seasons will often harbor large amounts of embedded shot (Pattee and Hennes 1983, Hennes 1985, U.S. Fish and Wildlife Service 1986). Differences in shotshell pellet burden in waterfowl have also been shown to exist among species (U.S. Fish and Wildlife Service 1986). In general, larger species usually carry greater shotshell pellet burdens than smaller species (U.S. Fish and Wildlife Service 1986), a phenomenon also suggested by our results.

The anatomical location of embedded shot in waterfowl at Galloway Bay was similar to what has been previously reported in other waterfowl species (Perry and Geisler 1980, Hennes 1985). The location of embedded shot may influence the availability of lead for foraging eagles. For example, Sabine and Klimstra (1985) and Hennes (1985) found that nonedible prey remains retrieved from eagle kill sites generally consisted of feathers and bones of the wings, pelvis, and vertebral column. Based on this and on observations of feeding eagles, Hennes (1985) estimated that 75–85% of embedded shot was available to eagles; the remaining shot, such as that deeply embedded into large bones, were considered unavailable as eagles rarely consumed these parts. Our results suggested a similar phenomenon, where 73% of embedded shotshell pellets were considered available to eagles.

Eagles may also secondarily consume lead shotshell pellets that were originally ingested by waterfowl (Locke and Thomas 1996). Although it was difficult to determine whether shotshell pellets in the lumen resulted from gunshot or ingestion (Lumiej and Scholten 1989), data from dead or moribund waterfowl at Galloway Bay indicated a low prevalence of shot in the ventriculus. In Saskatchewan, the proportion of waterfowl with ingested lead shotshell pellets have been reported as generally low (<4%) (Hochbaum 1993, Scheuhammer and Norris 1995). Field hunting, wide dispersal of

hunters, and annual cultivation of fields, as occur at Galloway Bay, all act to decrease the availability of lead shot pellets for waterfowl (Hochbaum 1993). Waterfowl in Saskatchewan do not appear to be overly exposed to lead based on surveys of lead content in wing bones (Dickson and Scheuhammer 1993). Therefore, it seems unlikely that eagles at Galloway Bay secondarily consume shotshell pellets originally ingested by waterfowl.

In comparison to other studies that have examined the castings of Bald Eagles that have been feeding on waterfowl (e.g., Griffin et al. 1982, Bengston 1984, Hennes 1985, Nelson et al. 1989), the frequency of castings with shotshell pellets at Galloway Bay was relatively low. While Bengston (1984) argued that castings with shotshell pellets are the best indicators of lead exposure for raptors, Hennes (1985) suggested that shotshell pellets in eagle castings represent a minimum estimate of the true ingestion rate.

Pain et al. (1993 and 1997) and Mateo et al. (1999) noted that the prevalence of lead shotshell pellets in castings of Marsh Harriers (*Circus aeruginosus*) increased with the progression of the hunting season and was higher within than outside the hunting season. However, no temporal trend was detected at Galloway Bay or by Hennes (1985). Hennes (1985) suggested that multiple castings which may be regurgitated by individual eagles after feeding on larger carcasses such as geese may “dilute” the prevalence of ingestion of shotshell pellets and may have masked seasonal increases (Hennes 1985).

The relatively high prevalence of lead shotshell pellets found in waterfowl carcasses and thus, the potential for consumption by eagles contrasted with the apparent low rate of ingestion of shotshell pellets. Hennes (1985) suggested that the rate of ingestion by Bald Eagles would not equal the prevalence embedded in carcasses because of unavailability due to anatomical location; this may have occurred at Galloway Bay. Alternatively, eagles may have been able to detect embedded shotshell pellets within the prey item and avoid them (cf. Stendell 1980). Possible evidence for this occurring at Galloway Bay was observed in one salvaged carcass of a White-fronted Goose that was almost completely defleshed, yet contained several ($N = 4$) shotshell pellets lying between bones in the ventral aspect of the synsacrum and vertebral column.

In an early review of the cases of lead poisoning in Bald Eagles, Feierabend and Myers (1984) in-

indicated that despite definitive diagnoses of lead toxicosis, only 14% of Bald Eagles necropsied in the United States had lead shotshell pellets present in the gastrointestinal tract. Therefore, lead toxicity or exposure in raptors cannot be ruled out solely on the basis of radiographic evidence (Janssen et al. 1986, Langelier et al. 1991), nor can the presence or absence of lead in the ventriculus be used to estimate quantitative lead concentrations (Kramer and Redig 1997). Since ingested shotshell pellets may rapidly erode, dissolve or be voided in the feces leaving no direct evidence of recent ingestion (Bellrose 1959, Scanlon et al. 1980), estimates of shotshell pellet ingestion determined from fluoroscopy likely represent a minimum estimate of actual prevalence and subsequent severity of exposure (Anderson and Havera 1985).

Given the relatively low prevalence of lead exposure (Miller et al. in press) and ingestion of shotshell pellets at Galloway Bay, eagles may be consuming more uncontaminated prey than indicated by our results (Miller et al. 1998). For example, nonanserid species such as American Coots are hunted less intensively and generally have a low prevalence of tissue-embedded shotshell pellets (U.S. Fish and Wildlife Service 1986). Therefore, the lower prevalence of lead ingestion by eagles at Galloway Bay may be partially attributable to the presence of a high proportion of coots in the diet. Moreover, in 1992 and 1995, eagles extensively fed upon moribund or dead waterfowl resulting from an avian cholera epizootic, a source likely to contain less lead shotshell pellets than waterfowl shot by hunters (Miller et al. 1998). Median PbB concentrations in eagles from 1992–95 did not, however, yield any significant differences between years (Miller et al. in press).

Reducing availability of lead shotshell pellets for raptors has long been the focus of management strategies for abating lead exposure amongst these species (Pattee and Hennes 1983, Feierabend and Myers 1984, U.S. Fish and Wildlife Service 1986, Pain et al. 1997). However, in light of recent findings (Kramer and Redig 1997, Miller et al. 1998), other sources of lead such as fragments from rifle bullets, fishing sinkers and lead shotshell pellets in upland game birds may be important. To accurately assess the effect on raptors of banning lead shotshell pellets for waterfowl hunting in the United States in 1991 and Canada in 1999, the importance of other potential sources of lead must be resolved (Elliott et al. 1992).

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STAND STRUCTURES USED BY NORTHERN SPOTTED OWLS IN MANAGED FORESTS

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ABSTRACT.—We compared vegetative structures in 4–16-ha patches in forest stands used by 12 pairs of Northern Spotted Owls (*Strix occidentalis caurina*) for nesting ($N = 44$) and foraging ($N = 38$) with habitat structures in 50 stands located randomly throughout annual home ranges in a young and mid-successional forest landscape (25–79 yr-old stands) in the foothills of the western Cascades in Oregon. Forest stand structures influenced selection for stands used for foraging and nesting by Spotted Owls, and abundance of these structures varied with successional development as represented by five age classes. Conifer saplings (10–19 cm in diameter at breast height [dbh]) and trees 50–79 cm dbh were more abundant in foraging areas than nest sites or random sites. Large snags (>40 cm dbh) tended to be more abundant, down woody debris was more abundant, and cover of herbs and low-growing shrubs (<0.5 m) was lower in stands in which owls hunted frequently than in randomly located stands of the same age classes. Owls nested in trees as young as 41 yr old, although 65% of nest trees were older than 120 yr of age. We found 22 (50%) nests in forest stands 46–79 yr of age, whereas owls repeatedly foraged in stands as young as 27 yr of age. Silviculturists should be able to create foraging habitat for Northern Spotted Owls in managed forests by emphasizing control of tree densities and form, woody debris, and understory vegetation. Suitable nesting habitat might best be facilitated via retaining legacy trees. Future research should determine the relative contribution of managed forests to owl conservation.

KEY WORDS: *Northern Spotted Owl*; *Strix occidentalis caurina*; *foraging habitat*; *managed forests*; *nesting habitat*; *Oregon*.

Estructuras de árboles utilizadas por *Strix occidentalis caurina* en bosques manejados

RESUMEN.—Comparamos las estructuras vegetales de 4–16 parches de bosques utilizados por 12 parejas de *Strix occidentalis caurina* en hábitats de anidación ($N = 44$) y forrajeo ($N = 38$), en estructura de hábitats de 50 parcelas de árboles ubicados al azar a lo largo de los rangos de hogar anuales en paisajes de sucesiones de bosques jóvenes (25–79 años), los cuales estaban ubicados en el piedemonte al oeste de Cascadas en Oregon. Las estructuras de árboles influenciaron la selección de árboles utilizados para el forrajeo y anidación de los búhos. La abundancia de estas estructuras varió con el desarrollo sucesional representado por 5 clases de edad. Las muestras de coníferas (10–19 cm) de diámetro a la altura del pecho (dap) y de árboles 50–79 cm dap fueron más abundantes en áreas de forrajeo que en los sitios de anidación o los sitios escogidos al azar. Los troncos grandes (>40 cm dap) tendían a ser más abundantes, la cobertura de hierbas y arbustos del sotobosque (<0.5 m) fue menor en los fragmentos de árboles en los que los búhos cazaban con frecuencia que en las estructuras de la misma clase de edad ubicadas al azar. Los búhos anidaron en árboles jóvenes de 41 años de edad, aunque el 65% de los árboles con nidos fueron de más de 120 años de edad, mientras que los búhos forrajearon repetidamente en árboles de 27 años de edad. Los silviculturistas podrían crear hábitat de forrajeo para los búhos en bosques manejados enfatizando el control de las densidades de árboles, su forma, y de la vegetación del sotobosque. El hábitat de anidación apropiado puede ser implementado protegiendo los árboles valiosos. Las investigaciones futuras deben determinar la relativa contribución de los bosques manejados a la conservación de los búhos.

[Traducción de César Márquez]

Field studies have repeatedly demonstrated that Northern Spotted Owls (*Strix occidentalis caurina*)

selectively use late-successional and old-growth (LS/OG) forest stands (Forsman et al. 1984, Carey et al. 1990, Hunter et al. 1995), and that vegetative structures within such stands likely influence selection of foraging habitats (Solis and Gutiérrez 1990, Call et al. 1992) and nest sites (Forsman et al. 1984,

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Buchanan et al. 1993, Buchanan and Irwin 1995, LaHaye and Gutiérrez 1999). North et al. (1999) documented that forest stand structures influenced selection of foraging sites used by Northern Spotted Owls in unharvested forests in Washington. Forest stand structures, including large trees and snags, multiple canopy layers, downed woody debris and shrubs, have been hypothesized to provide favorable microclimates, nest sites, cover from predators, and/or habitat for the owl's prey (Carey 1985, Carey and Johnson 1995, Carey and Peeler 1995). Forest stand structures influence small mammal diversity and abundance (Carey 1995), and many aspects of Spotted Owl biology are influenced by prey abundance, diversity and biomass (Carey et al. 1992, Carey and Peeler 1995, Ward et al. 1998, Carey et al. 1999).

There are no detailed measures of forest stand structures and other habitat attributes in young or managed forests occupied by Northern Spotted Owls. Investigators who have documented Northern Spotted Owl presence in young and mid-successional (Y/MS) forests (defined herein as those 25–79 yr of age) have speculated that such occupancy probably is related to structural legacies from previous, older forests (e.g., Forsman et al. 1977, Irwin et al. 1989). Information on density or abundance of vegetative structures associated with use of Y/MS forests by Northern Spotted Owls could be used for crafting silvicultural prescriptions for producing or enhancing habitat in managed forests, if a breeding population of owls could be found occupying a Y/MS forest landscape. We located such a Y/MS landscape occupied by Northern Spotted Owls at the foot of the Cascade Range in western Oregon, where surveys identified 57 territories occupied by 42 owl pairs and 15 single owls (with annual variation) near Springfield, Oregon in a managed landscape that contained <10% LS/OG forests. Owl pairs at 29 of the 42 sites successfully fledged young 1 yr from 1992–99, providing an opportunity to examine forest stand structure at foraging and nest sites.

The scale for comparing used and available habitats determines the range of inferences from habitat selection studies (Johnson 1980, Porter and Church 1987). Previous investigators (Laymon and Reid 1986, Carey and Peeler 1995) found that Northern Spotted Owls often concentrated their searches for prey repeatedly in small "pockets" (<16 ha) of forests, and Bingham and Noon (1997) recommended sampling habitat conditions

within core areas (Samuel et al. 1985), or those areas within home ranges that receive disproportionate use. Quantifying habitat components in frequently-used stands, which are most likely to occur within core areas, may help identify consistent aspects of the environment that trigger the owl's habitat selection response and influence its survival and reproduction (Bingham and Noon 1997). Thus, our primary goal was to evaluate stand structural factors associated with forests used for nesting and foraging in frequently-used areas within owl home ranges. We wanted to learn if densities of forest stand-structures and other habitat descriptors differed across a successional gradient and among nest sites, foraging areas, and random locations within owl home ranges.

STUDY AREA

The study area was bordered by the Willamette National Forest on the east and forests adjacent to Interstate Highway-5 on the west, and extended south from Brownsville in Linn County to Dorena Reservoir in Lane County, Oregon. About 10% of the land was administered by the USDI Bureau of Land Management (BLM). The remainder was owned by private timber companies or occurred as rural residential areas and farmlands. Forests in the northern and western portions of the study area regenerated following timber harvests that often left scattered nonmerchantable trees or seed trees, many of which were >80 cm in diameter. Forests in the eastern parts of the study area regenerated following extensive wildfires about the turn of the century (Teensma 1987).

The 57 owl territories that we identified lay below 915 m in elevation in the foothills of the McKenzie River drainage. The area was in the Western Hemlock Zone (Franklin and Dyrness 1981), and the forests were predominantly coniferous trees such as Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Common hardwoods included Pacific dogwood (*Cornus nuttallii*), big leaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). Less common species included golden chinquapin (*Castanopsis chrysophylla*) and Pacific yew (*Taxus brevifolia*). Common understory species included swordfern (*Polystichum munitum*), salal (*Gaultheria shallon*), vine maple (*Acer circinatum*), and Oregon grape (*Berberis nervosa*).

METHODS

Radiotracking of 26 owls in the Springfield population provided an opportunity to examine habitat structures at areas of concentrated use for foraging. We also examined forest stand structures at nest sites. Capturing and radiotracking Spotted Owls followed procedures described by Carey et al. (1989, 1990) and Guetterman et al. (1991). To ensure statistical independence, only telemetry locations separated by 72 hr were used in the analysis (Guetterman et al. 1991). This criterion was met by field crews locating radio-tagged owls 2–3 times per week. We used only owls for which telemetry data were gathered contin-

uously according to that schedule for >1 yr (13–27 mo), to provide estimates of year-round use patterns within home ranges. Nocturnal telemetry locations (when owls foraged most frequently) were initially mapped in the field on 7.5-min U.S. Geological Survey quadrangle maps and on aerial photographs. We subsequently mapped owl home ranges and identified core areas using the adaptive kernel (ADK) method (Worton 1989, 1995). Although core areas of Northern Spotted Owls may include up to 75% of the telemetry locations of an individual or pair (Bingham and Noon 1997), we used the 60% ADK isopleth to estimate core area.

Using aerial photographs, we identified forest stands for sampling stand-structural measurements using three criteria: the radio-tagged owls involved were members of pairs of territorial Spotted Owls, at least one of which was monitored for 1 yr; the pairs nested successfully ≥ 1 time during the study; and the stands received repeated or disproportionate use by radio-tagged owls for foraging, which we arbitrarily defined as 4% of the total telemetry locations in areas that comprised 1% of the annual ADK home range. Due to the concentration of use near the center of the home ranges (Rosenberg and McKelvey 1999), such repeatedly-used foraging areas were located within core areas. Sizes of foraging areas sampled varied with the number of telemetry locations and size of error polygons from telemetry, and ranged from 5–15 ha, usually 10 ha. We specified the maximum sampling area at 15 ha based upon similar observations by Laymon and Reid (1986) and Carey and Peeler (1995), as well as our own observations. Also, we specified the minimum foraging area to be at least twice the size of average telemetry-error polygons (1.5–2.0 ha), which we estimated by comparing triangulations with actual (walk-in) observations ($N = 75$) of radio-tagged birds. Although our choice of 4% of telemetry points in 1% of home ranges was arbitrary, the design was similar to that of North et al. (1999), who used 3–9% of telemetry locations to designate “moderately-used” stands and 10% for very highly-used stands. However, they sampled stands 40–80 ha in size, whereas we sampled within much smaller areas that contained a comparatively high density of telemetry points.

We sampled 2–4 frequently-used foraging areas within each core area; few home ranges contained >4 repeatedly-used foraging areas. Thus, the foraging area (or nest site) was the sampling unit, not each owl. North et al. (1999) found that variance in stand structure estimates stabilized at 3–4 plots per stand in homogeneous stands. Thus, we sampled 2 plots in each foraging area or random site, but opted for five plots when we encountered additional variation, as was found in the largest stands sampled (15 ha) and also in those with large-tree legacies from previous stands. Data presented are averages from 104 plots sampled in 38 frequently-used foraging areas within home ranges of 12 pairs of Northern Spotted Owls, either from combined home ranges of both pair members or from one member of a pair. In addition, we collected data from 44 nest stands, using the nest tree as the center of a single plot. Several owl pairs used more than one nest tree; alternate nest trees were sampled only if they were found in different stands.

Specific locations of plots to be sampled within forag-

ing areas and in comparison areas that contained zero or low densities of telemetry locations were established using random coordinates on grid maps (100-m grid intervals) and found in the field using a global positioning system. Statistical comparisons of data from nests and foraging areas were made with data gathered from 50 stands (averaged from three plots/stand) that were selected randomly. The 2–4 foraging stands sampled within individual home ranges were >200 m apart to ensure a broad distribution and sampling of the range of types within home ranges, and we also assumed that the random sites within the 12 home ranges represented the range of variation in habitat conditions used by Spotted Owls in the study area. Examples of home ranges, core areas, and sampling design for estimating habitat structures at frequently-used foraging sites and random sites are shown in Fig. 1.

We sampled several variables associated with four major stand-structural features that are believed to be important to Spotted Owls and/or their prey: densities and sizes of live trees; coarse woody debris, including fallen logs and snags; understory vegetation; and forest canopy structure. Our sampling design employed nested circular plots, following procedures used in Spies (1989) and North et al. (1999), in which the minimum vegetation structure size sampled increased with plot size. These procedures provided tallies of large, infrequently occurring items such as snags and old-growth trees without over-sampling small, less variable structures. Each plot included three nested circular sub-plots: 0.05-, 0.10-, and 0.20-ha in size.

Beginning 2 m from the site center, we made ocular estimates of cover (to the nearest percent) for shrubs and herbs in three height classes (<0.5, 0.5–2.0, and >2.0 m) in four 4-m² quadrats placed in the cardinal directions. We counted all living trees and all snags (>10 cm dbh) and estimated abundance and length of downed woody debris (pieces >10 cm diameter) within the 0.05-ha sub-plot. In the 0.1-ha plot, we tallied living trees 51–80 cm dbh and all downed logs (large and small diameter and length). Finally, in the 0.2-ha plot, we recorded the number of large snags (50 cm dbh) and large living trees (80 cm dbh). We also estimated stand age (from annual growth rings), average crown depth (using a clinometer), and average crown volume ($\frac{1}{3}\pi r^2 \times \text{height}$) based upon six living dominant or codominant trees that we judged to typify the dominant canopy trees in each stand sampled. We estimated canopy cover using a concave densitometer (after this study was well underway, we learned that this tool inflates estimates in high closure classes, see Cook et al. 1995). Distance from the ground level to the lower canopy provided an index to flying space under the primary canopy. We sampled only those stand-age classes that owls used for nesting or that radio-tagged owls used repeatedly for foraging. Thus, we discarded random points that fell on non-forested areas or forest age-classes that were not used. For statistical comparisons, we grouped stands into five age classes that approximated a successional gradient: 25–39, 40–59, 60–79, 80–119, and >120 yr. We designated the first three age classes as Y/MS or managed forests and the older two as LS/OG forests.

After evaluating stand structure variables to assess nor-

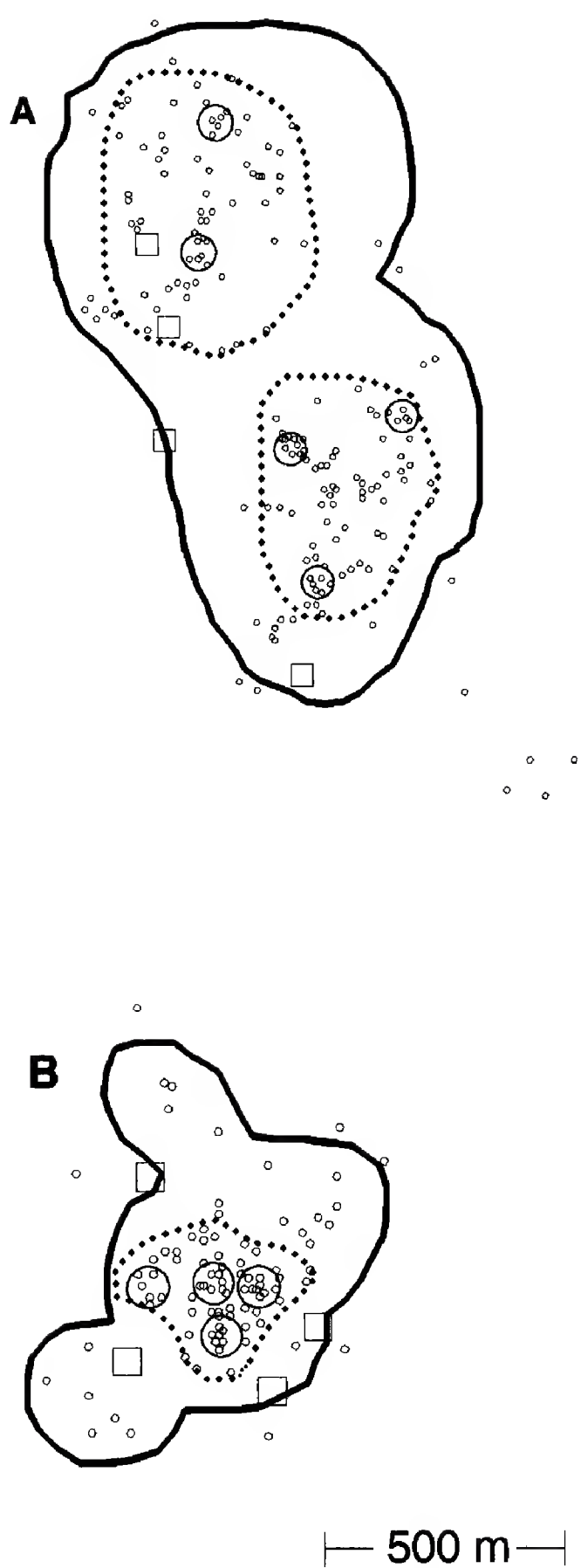


Figure 1. Examples of sampling design for comparing habitat structure at frequently-used foraging areas (large circles) within core areas (dotted lines) of a pair of Northern Spotted Owls (A) and an individual Spotted Owl (B) with that at randomly-located areas (squares). Radiotelemetry points are denoted by small circles and 95% adaptive kernel home ranges are enclosed by solid lines. Both members of the pair in A used two core areas that were separated by unusable habitat.

Table 1. Number of forest stand samples by age class for repeatedly-used foraging sites and nesting sites of Northern Spotted Owls and random sites within Spotted Owl home ranges, western Oregon. Age classes 25–39, 40–59, and 60–79 yr were classified as young or mid-successional (Y/MS) stands and classes 80–119 yr and >120 yr were late-successional and old-growth (LS/OG) stands.

	FOREST STAND AGE CLASS (yr)					TOTAL
	25–39	40–59	60–79	80–119	>120	
Foraging	5	16	5	8	4	38
Nesting	0	11	11	18	4	44
Random	19	10	7	9	5	50

quality of distributions and possible correlations, we tested for effects of succession with a two-way, fixed effects analysis of variance (ANOVA). For comparisons that were statistically significant, Fisher’s least significant difference test was used to determine which levels differed. Comparisons among random, foraging, and nesting sites were made using fixed effects ANOVA. In general, we considered comparisons statistically significant if Type-I error levels were <0.05.

RESULTS

Descriptive Data. Core areas of Northern Spotted Owls for which we obtained sufficient telemetry data averaged 372 ha (SE = 67.6 ha) in size for 18 individuals and 417 ha (SE = 128.9 ha) in size for 6 pairs, and occupied <25% of annual ADK home ranges among individuals and pairs. The 44 nests were in stands that ranged in age from 46–168 yr, half (22) of which were in LS/OG forests and half of which were in Y/MS forests (Table 1). These included 11 nests in stands 46–60 yr old. Trees with owl nests were mostly Douglas-firs (86%) of large size (73% >80 cm dbh) and relatively old age (65% >120 yr). Such trees clearly were legacies from previous stands. All but four nests were in living trees. Four nest trees were <60 yr old and <50 cm dbh, with the youngest being 41 yr. The nest structures that we could identify were either cavities (N = 17) or debris platforms (N = 22) on large limbs or in tree crotches.

Owls foraged in stands with a wider age range than was found at nest sites. Repeatedly-used foraging areas ranged from 27–>200 yr in age. Twenty-six Y/MS stands and 12 LS/OG stands were used repeatedly for hunting (Table 1). Five stands 25–40 yr of age were used repeatedly for foraging. Radio-tagged owls made very little use of stands <25 yr of age. Stand composition was similar to that of

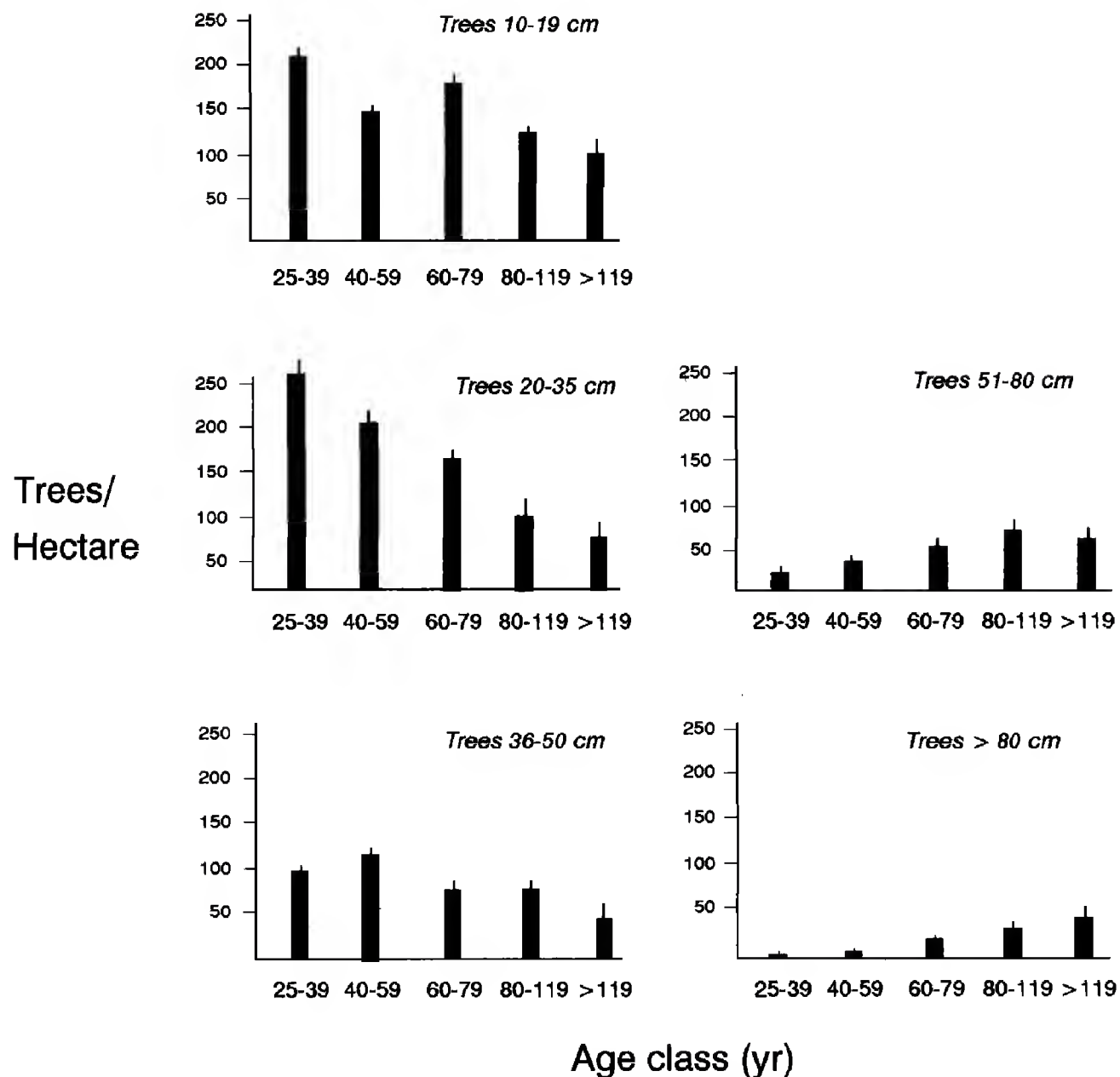


Figure 2. Successional patterns of tree densities by size- and age-class in stands frequently used for foraging or nesting or at random locations within home ranges of Northern Spotted Owls. Vertical lines above bars indicate standard errors.

Douglas-fir forests of western Oregon in that stands typically consisted of abundant, small-diameter western hemlock seedlings and trees (<20 cm dbh) with Douglas-fir tending to be the large-diameter trees.

Density of Live Trees. Average densities of trees seemed to differ among the five classes that we used to express successional gradients. Stands 25–39 yr of age contained highest densities of trees <35 cm dbh. Stands 40–79 yr of age contained moderate densities (>40/ha) of trees >50 cm dbh and mature and older stands (80 yr old) contained relatively high densities of large trees with >19 trees/ha >80 cm dbh (Fig. 2). In general, densities of trees in the three diameter classes <50 cm declined with advancing age and densities of trees >50 cm dbh increased. Nearly all stands sampled

contained more than one large (>80 cm dbh) tree/ha.

We found relatively few differences in densities of trees of five diameter classes among nesting, foraging, or random sites within owl home ranges (Table 2). Foraging sites contained more sapling trees (10–19 cm dbh) and more 51–80 cm dbh trees than either nesting or random sites. In turn, nest sites contained the most trees in the 20–35 cm dbh class and fewest in the 51–80 cm dbh class. Foraging sites tended to contain a few more large trees (>80 cm dbh) than random or nesting sites.

Snags and Downed Wood Debris. We found successional-related gradients in densities of large snags in comparisons that included all stands that we sampled (Table 3). Large snags increased and small snags tended to decrease with advancing

Table 2. Comparisons of tree densities by size class among nesting, foraging, and random locations within Northern Spotted Owl home ranges, western Oregon. Row values with different superscripts are statistically different at the indicated level of probability, based on ANOVA.

TREE SIZE CLASS (dbh in cm)	TREE DENSITY (No./ha ± SE)			P ^a
	RANDOM	FORAGING	NESTING	
10–19	120 ^a ± 16	186 ^b ± 19	162 ^c ± 17	0.041
20–35	164 ^a ± 13	142 ^b ± 16	188 ^c ± 14	0.109
36–50	87 ± 7	84 ± 8	79 ± 8	0.814
51–80	56 ^a ± 4	62 ^a ± 5	43 ^b ± 4	0.018
>80	15 ± 2	19 ± 2	15 ± 2	0.201

stand age and large snags generally were more abundant at foraging and nesting sites than at random, although the differences were not consistent among all age classes. There were no differences in densities of small-diameter snags among foraging, nesting, and random locations.

There were no clear successional gradients in the densities or volumes of downed woody debris (Table 4), although the youngest stands usually contained the least amount of woody debris. Foraging areas contained greater densities and vol-

umes of both large and small woody debris than random sites. Foraging areas also contained as much as 50% more downed trees than nest sites or random locations within home ranges. The volume of large woody debris was greater at nest sites than random sites and several significant comparisons occurred within age classes at foraging and nesting sites and random locations. Although estimates of the volume of woody debris were more variable than density estimates, foraging sites in managed stands contained from 150–200% more debris volume than random sites of the same age classes.

Canopy Structure. Canopies of all stands were dense, averaging >80% closure. Average crown volume increased with advancing stand age, but did not differ among foraging, random or nesting locations within home ranges, except that trees in the five foraging stands sampled that were 60–79 yr of age contained smaller crown volumes than those at random sites (Table 5). Tree crown volume was significantly lower at foraging sites than at random sites in stands <40-yr old. Average crown depth of trees at foraging sites was less than that in nest sites or random locations for stands <80 yr of age (i.e., Y/MS stands).

The index of flying space beneath the forest canopy increased with advancing stand age and was significantly less at foraging sites than at random sites within home ranges over all age classes com-

Table 3. Snag densities at Northern Spotted Owl foraging, nesting, and random locations, western Oregon.

AGE CLASS (yrs)	SNAG DENSITIES (No./ha ± SE)			<i>P</i> ^a	OVERALL
	FORAGING	NESTING	RANDOM		
Large Snags (≥50 cm dbh)					
25–39	4.4 ± 1.4	n.d. ^b	2.1 ± 0.6	0.1461	3.0 ± 1.3
40–59	2.5 ± 1.5	5.5 ± 1.9	6.1 ± 1.8	0.271	4.1 ± 1.1
60–79	7.0 ± 3.4	7.7 ± 2.3	2.6 ± 2.9	0.378	6.1 ± 1.3
80–119	12.0 ± 2.1	6.1 ± 1.3	9.6 ± 1.9	0.0575	8.3 ± 1.1
≥120	17.6 ± 4.1	12.5 ± 4.1	5.3 ± 3.7	0.1277	11.4 ± 1.7
Overall	7.0 ± 1.1	7.0 ± 1.0	4.7 ± 0.9	0.0165	
Small Snags (<50 cm dbh)					
25–39	129 ± 39	n.d. ^b	125 ± 18	0.9377	133 ± 16
40–59	112 ± 24	124 ± 29	171 ± 31	0.5442	130 ± 13
60–79	91 ± 13	91 ± 13	53 ± 16	0.5076	79 ± 16
80–119	111 ± 25	92 ± 17	77 ± 24	0.4722	88 ± 13
120	79 ± 30	70 ± 26	52 ± 23	0.5099	66 ± 21
Overall	108 ± 14	100 ± 12	126 ± 13	0.5012	

^a Probability values in same row do not differ, as determined from ANOVA.
^b No data.

Table 4. Average density and volume of large (>50 cm diameter) woody debris and volume of small (10–50 cm diameter) woody debris in Northern Spotted Owl foraging, nesting, and random sites, western Oregon.

AGE CLASS (yr)	FORAGING	NESTING	RANDOM	<i>P</i> ^a	OVERALL
Density of Large Woody Debris (No./ha ± SE)					
25–39	86 ± 27	n.d. ^b	65 ± 12	0.4816	77 ± 12
40–59	113 ± 16	73 ± 18	62 ± 19	0.1022	82 ± 10
60–79	147 ± 29	79 ± 19	66 ± 24	0.0987	95 ± 12
80–119	111 ± 21	76 ± 13	82 ± 19	0.3893	91 ± 10
120	139 ^a ± 22	55 ± 22	65 ± 20	0.0435	86 ± 16
Overall	117 ^a ± 10	74 ± 9	68 ± 8	0.0003	
Volume of Large Woody Debris (m ³ /ha ± SE)					
25–39	184 ± 55	n.d. ^b	125 ± 25	0.3377	186 ± 35
40–59	278 ± 41	143 ± 41	159 ± 50	0.0757	193 ± 28
60–79	368 ^a ± 73	197 ^b ± 49	115 ^c ± 62	0.0476	216 ± 35
80–119	243 ± 65	218 ± 40	103 ± 57	0.1932	197 ± 29
120	345 ± 132	344 ± 132	88 ± 114	0.2821	252 ± 47
Overall	281 ^a ± 28	206 ^b ± 25	123 ^c ± 23	0.0002	
Volume of Small Woody Debris (m ³ /ha ± SE)					
25–39	28 ^a ± 4	n.d. ^b	17 ± 2	0.0336	20 ± 3
40–59	19 ± 4	23 ± 4	16 ± 4	0.4706	19 ± 2
60–79	31 ± 6	19 ± 4	21 ± 5	0.2884	24 ± 3
80–119	39 ^a ± 6	17 ^b ± 4	23 ^b ± 5	0.0163	25 ± 92
120	39 ± 9	12 ± 9	16 ± 8	0.1357	22 ± 4
Overall	28 ^a ± 2	19 ^b ± 2	19 ^b ± 2	0.0031	

^a Probability values in same row do not differ, as determined by ANOVA. Row values with different superscripts are significant at the level of probability indicated.
^b No data.

Table 5. Comparison of canopy structure in stands used for foraging and nesting with random locations within Northern Spotted Owl home ranges, western Oregon.

AGE CLASS (yr)	FORAGING	NESTING	RANDOM	<i>P</i> ^a	OVERALL
Average Crown Volume (m ³ ± SE)					
25–39	197 ^a ± 61	n.d. ^b	303 ± 31	0.0337	226 ± 47
40–59	253 ± 30	228 ± 98	352 ± 49	0.1309	282 ± 38
60–79	292 ^a ± 89	373 ^b ± 88	571 ^a ± 75	0.0369	424 ± 47
80–119	489 ± 84	477 ± 69	491 ± 79	0.9857	487 ± 39
120	716 ± 112	246 ± 147	641 ± 101	0.6344	536 ± 63
Overall	349 ± 36	376 ± 38	418 ± 32	0.1564	
Average Crown Depth (m ± SE)					
25–39	12.7 ^a ± 1.4	n.d. ^b	17.0 ± 0.7	0.0113	15.4 ± 1.0
40–59	14.0 ^a ± 0.5	17.1 ^b ± 1.1	17.2 ^b ± 0.7	0.0012	16.0 ± 1.1
60–79	14.4 ^a ± 1.2	18.6 ^b ± 2.5	21.3 ^b ± 1.0	0.0013	18.0 ± 1.0
80–119	18.6 ± 1.1	20.2 ± 2.0	19.0 ± 1.5	0.843	19.0 ± 1.1
120	20.4 ± 1.6	14.5 ± 4.0	20.2 ± 1.5	0.9161	18.1 ± 1.5
Overall	15.5 ^a ± 0.6	18.3 ^b ± 1.3	18.3 ^b ± 0.5	0.0006	

^a Probability values do not differ, as determined from ANOVA.
^b No data.

Table 6. Average distance from ground to lowermost whorls of branches on trees at Northern Spotted Owl foraging, nesting, and random locations, western Oregon.

AGE CLASS (yr)	AVERAGE DISTANCE (m ± SE)			<i>P</i> ^a	OVERALL
	FORAGING	NESTING	RANDOM		
25–39	13.0 ± 2.0	n.d. ^b	16.2 ± 1.0	0.165	12.3 ± 1.1
40–59	13.8 ^a ± 0.9	16.4 ^b ± 1.3	20.2 ^c ± 1.2	0.0003	16.6 ± 0.8
60–79	18.3 ± 2.7	15.7 ± 1.5	19.9 ± 2.3	0.657	17.9 ± 1.1
80–119	22.2 ^a ± 1.8	17.4 ^b ± 1.1	29.0 ^c ± 1.7	0.0148	22.1 ± 0.9
>120	21.2 ± 3.5	22.9 ± 2.4	31.4 ± 3.1	0.0681	25.3 ± 1.4
Overall	16.8 ^a ± 1.1	17.4 ^a ± 1.2	21.3 ^b ± 1.0	0.0026	

^a Probability foraging, nesting, and random values do not differ, as determined by ANOVA.
^b No data.

bined and for stands in the 40–59 and 80–119 year categories (Table 6). The same was true for nest sites in overall comparisons with flying space tending to be less at nest sites.

Understory Vegetation. We found no clear successional trends in understory vegetation cover. Cover of understory vegetation <0.5-m tall was significantly less at foraging locations than at random

locations for most age classes (46.0 vs. 65.3%, *P* = 0.001), but understory vegetation cover at nest sites generally did not differ from that at random locations (Fig. 3, 66.2 vs. 65.3%, *P* = 0.894). Understory cover in the other two height classes was more variable. In separate ANOVA comparisons that pooled stands in the two broader classes of Y/MS and LS/OG forests, foraging locations contained

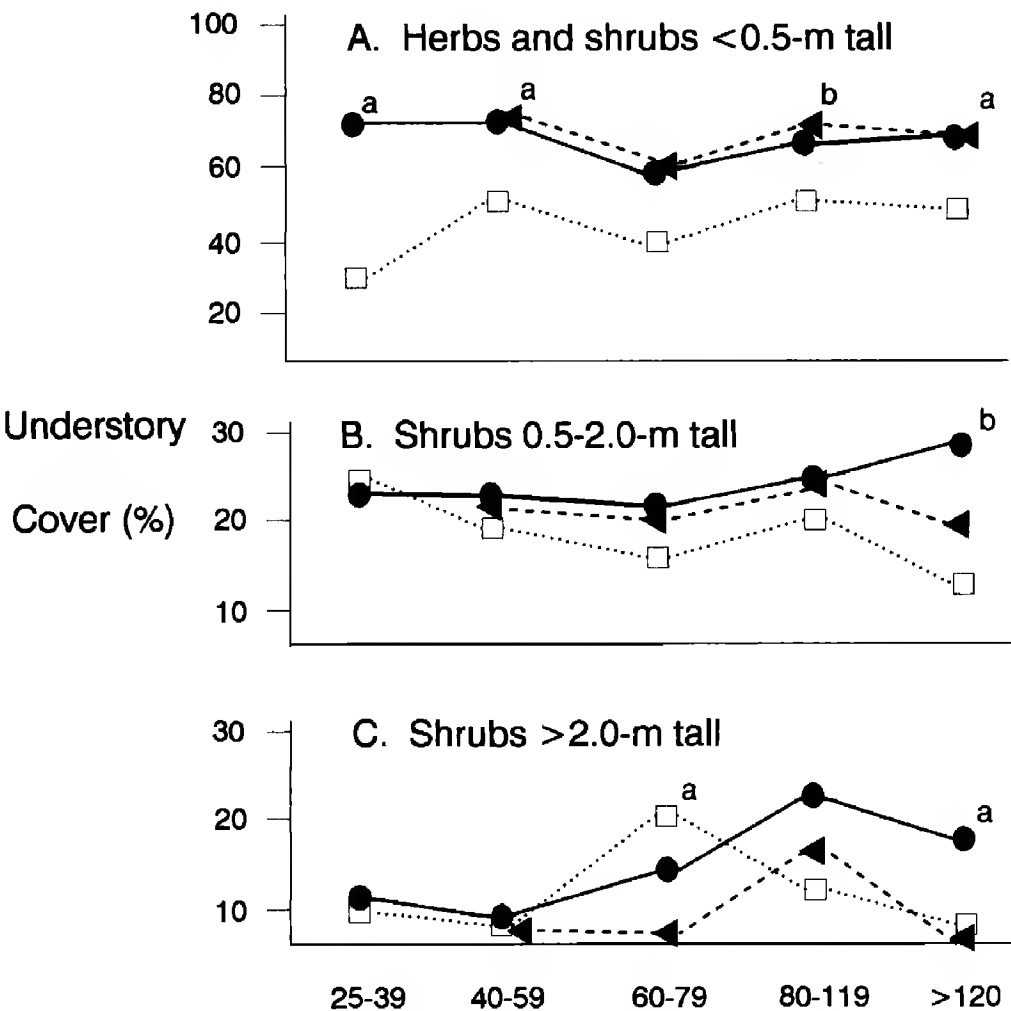


Figure 3. Comparisons by ANOVA of successional trends among foraging areas (squares), nest sites (triangles), and random locations (dots) for three understory cover classes within Northern Spotted Owl home ranges. Superscripts indicate within-age class comparisons that were statistically different at Type-I error probabilities of <0.05 (a) and 0.05–0.10 (b).

less understory vegetation cover 2.0 m in height than did nest sites and random locations in Y/MS forests (64.3% vs. 89.2% and 89.6%, $P < 0.040$). Understory cover at nest sites did not differ from random locations within Y/MS and LS/OG classes.

DISCUSSION

Most forest stand structures increased in abundance with advancing forest succession and probably influenced the choice of Y/MS forests by Northern Spotted Owls for nesting and foraging habitats. The most important stand structures in influencing habitat use were the amount of woody debris and, less consistently, the number of large snags at foraging sites and large-diameter trees at nest sites. The direct connection of standing and downed dead trees to owl biology probably occurs through the relationship between dead wood and the owl's prey. This appears particularly likely for northern flying squirrels (*Glaucomys sabrinus*), which are associated with snags (Carey 1995) and are the primary prey for owls in forests similar to those we studied (Forsman et al. 1984). Northern flying squirrel abundance in Y/MS forests may equal that of LS/OG forests if old-forest legacies (i.e., large trees and snags and downed wood debris) are present and understory vegetation is relatively well-developed (Carey 1995). Many other small forest mammal prey of Spotted Owls also are associated with coarse woody debris on the forest floor (Maser and Trappe 1984, Carey 1995, Carey and Johnson 1995), such as woodrats (*Neotoma* spp.), deer mouse (*Peromyscus maniculatus*), Townsend's chipmunk (*Tamias townsendii*), and western red-backed vole (*Clethrionomys occidentalis*).

Although owl foraging occurred in a broad array of structural conditions across all successional spectra, conditions of nesting sites were more specific. For example, foraging occurred in stands as young as 27 yr, whereas nesting occurred in stands >45 yr. Further, 50% of the nests were in LS/OG stands, which comprised $<10\%$ of the study area, and trees containing nests in Y/MS stands were often much older than trees that typified the nest stands. Finally, understory vegetation <2.0 -m tall did not influence nest-site choice but did influence use of foraging sites.

Densities of live trees and small and large snags varied with advancing succession at sites used frequently for foraging, which was expected due to competition among trees during the course of forest development (Oliver and Larson 1990). There-

fore, most of the stands we sampled were classified as within the stem-exclusion or understory reinitiation phases (Oliver and Larson 1990) of forest succession. However, most of the repeatedly-used foraging stands also contained structural legacies from previous forests, including large trees, large snags and large woody debris, and many nesting sites classified as being in 60-, 80-, or 120-yr old stands met several of the structural components defining old-growth forests in the Western Hemlock Zone (Franklin et al. 1981, Old-Growth Definition Task Group 1986). Similarly, densities of trees 80 cm dbh in most of the stands >80 yr of age met the large-tree criterion of the definition of old-growth forests, or 20 such large trees/ha (Franklin et al. 1981, Old-Growth Definition Task Group 1986). In fact, some of the stands that were 60–79-yr old also contained enough trees 80 cm dbh to meet the large-tree criterion used to define old-growth forest. This was particularly true for 60–79-yr old, repeatedly-used foraging stands which averaged 19 large trees/ha. Such large-diameter trees were not necessarily old, although some were old-growth residuals from previous stands, and others were broken-topped, old-growth western hemlock trees that did not protrude through the overstory canopy.

Because sites that we measured were used frequently for foraging or for nesting and were within core areas (i.e., areas disproportionately used within home ranges), structural features of stands might be important determinants of habitat selection of Northern Spotted Owls. Indeed, several variables exhibited little variation across all age classes of stands within core areas. All stands that were repeatedly used contained dense forest canopies ($>80\%$ cover, as estimated by a spherical densitometer) and had well-developed understory vegetation. All but the youngest sites contained large volumes of coarse woody debris, 1 large snag/ha, and at least a few live trees >80 cm in diameter. "Flying space," which varied as expected with advancing succession, was consistently lower at foraging and nesting sites than at random locations.

We were not certain why "flying space" was lower at foraging sites, even though tree diameters and crown volumes were the same as at random locations. It was possible that the lower-slope positions and east and northern aspects of foraging sites may have influenced the development of tree crowns there because of the limited amount of sunlight they receive. In such topographic conditions,

trees do not self-prune as rapidly as in other topographic settings (Oliver and Larson 1990), so flying space would be lower. In this case, the reduced flying space in foraging sites was simply a consequence of their use of lower topographic locations in the habitat.

We are also unsure what can be inferred from the information on understory vegetation cover, the total of which generally was less at foraging sites than at random and nesting locations. The differences did not appear to be caused by variation in sampling nest sites. Our results were contrary to those of Carey (1995) who suggested use of silvicultural manipulations to increase ericaceous shrubs which would accelerate growth of Northern Spotted Owl habitat in areas where LS/OG is lacking, but they were similar to those of Solis and Gutiérrez (1990) who found less shrub and herb cover at frequently-used Northern Spotted Owl foraging sites in northern California and those of Call et al. (1992) who found less herbaceous cover at owl sites than random locations for California Spotted Owls (*S. o. occidentalis*). We presume that Spotted Owl response to understory vegetation may be unimodal or asymptotic with gradients of understory vegetation cover and with variation in abundance or access to small mammal communities. There is evidence of such nonlinear responses by small mammals to gradients of understory vegetation density and composition (Carey 1995). If so, it seems possible that understory vegetation can be either too sparse, resulting in low prey densities, or too dense, thereby impeding access by owls to prey. The management application of this is to maintain patchy understories providing prey that are both abundant and accessible to owls.

Northern Spotted Owls used Y/MS forests substantially more frequently than reported by Forsman et al. (1984) and Carey et al. (1990) for Spotted Owl home ranges elsewhere in western Oregon. Such differential use of habitats by raptors may be due to local and structural differences in preferred habitats (Mosher et al. 1986). In the managed-forest landscape that we studied, stand structural differences were the most important habitat features determining use by Northern Spotted Owls. For example, turn-of-the-century wildfires left large legacy trees and timber harvesting about 60 yr prior to our study left cull or seed trees across the landscape. Both types of disturbance provided numerous snags and downed structural

legacies. Also, the area contained frequent pockets of root-rot (*Armillaria* spp.) that resulted in large piles of downfall.

We believe our information merits judicious application in forest management strategies, which increasingly strive to protect wildlife by applying information from stand- to landscape-levels. Recent examples include the conservation strategy for federal timberlands in the range of the Northern Spotted Owl (Thomas et al. 1993) and that described by Hicks et al. (1999) for managed, private timberlands. Doing so requires an understanding of both the diversity of forest stand structures used by owls and silvicultural procedures than can create them within the context of natural disturbance and timber management. Northern Spotted Owls apparently discriminate and select among Y/MS stands on the basis of stand-structural differences; therefore, providing these structures should be important parts of prescriptions for enhancing the value of young stands. Our information could help forest managers assess the value of future habitat, allowing them to schedule management activities across landscapes. We believe that extensively-managed Y/MS landscapes could contribute significantly to the long-term persistence of Northern Spotted Owls. Until such contributions are demonstrated to support viability, we strongly caution against drawing the inference that Y/MS forests with structural legacies might be an equivalent substitute for LS/OG forests.

Solis and Gutiérrez (1990) predicted that studies of Northern Spotted Owls in managed landscapes would show use of habitats that structurally resemble old-growth forests. Indeed, we found that Spotted Owls selected large, old trees for nests and that they selected foraging areas on the basis of coarse woody debris and understory vegetation in a managed landscape dominated by Y/MS stands. This information provides additional support for habitat restoration as part of a strategy for recovery of the Northern Spotted Owl (Carey 1995) and for blending goals of a forest-based economy with those of a healthy biotic community.

Silvicultural prescriptions could accelerate development of habitat for owls and perhaps other species that frequent LS/OG forests. We suggest that foraging habitat should contain seven large (40 cm dbh) snags/ha and 280 m³/ha of coarse woody debris, based on averages for 26 repeatedly-used sites in Y/MS forests in forest patches 16 ha in size. These values are similar to those of North

et al. (1999), who worked with Northern Spotted Owls in unmanaged forests and those of Buchanan et al. (1999), who recommended some 10 large snags/ha based upon 16 telemetry points in young forests in western Washington. Noting that both small- and large-diameter woody debris apparently influenced use for foraging, we wonder if equivalent amounts of small-diameter logging residue might be piled to create woody debris. Doing so would constitute a topic for experimental research. Foraging success by Northern Spotted Owls may be optimal in stands with a mix of canopy gaps and patchy ground cover (Carey 1995). Thus, precommercial thinnings in patches might support foraging in such areas by maintaining understory vegetation (Omule 1988, Carey and Curtis 1996), as long as total understory cover does not exceed about 75–80%. Skillful applications are required in our area because salal (*Gaultheria shallon*) may quickly form dense patches that exclude both herbaceous and tree-seedling establishment (Huffman et al. 1994). Nesting habitat involves more advanced successional development. Silvicultural prescriptions for providing suitable nest sites in managed forests could be facilitated by thinning to low densities (Tappeiner et al. 1997) and retaining small patches (perhaps 4 ha) that include large legacy trees. We recommend prescriptions that can ensure presence of 4 such trees/ha after a stand age of 40 yr, based upon the observation that only a few nesting stands contained <3 trees/ha >80 cm dbh. Because physical features such as topography and elevation influence use of foraging sites by Spotted Owls (Haufler and Irwin 1993), silvicultural manipulations should vary with topographic conditions. For example, we found that Spotted Owls used areas on the lower half of slopes and near riparian areas most often for foraging (Irwin 1994). Carey and Peeler (1995) also found significant use of lower-slope positions by Northern Spotted Owls in western Oregon. Therefore, management of these areas should be site-specific to ensure their integrity.

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POPULATION FLUCTUATIONS OF THE HARRIS' HAWK (*PARABUTEO UNICINCTUS*) AND ITS REAPPEARANCE IN CALIFORNIA

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ABSTRACT.—The Harris' Hawk (*Parabuteo unicinctus*) was considered extirpated from California in the mid-1960s. Most sightings in the past 30 years were, therefore, considered to be escaped or released birds. The species has recently staged an incursion into southern California and northern Baja California in the 1990s, involving nearly 50 individuals and local breeding. This incursion was apparently another in a long-term series of population fluctuations of the Harris' Hawk, each bringing large numbers to the north and west of its established range in Arizona and Baja California. Although first recorded at the state border in the 1850s, the Harris' Hawk was not recorded as a breeder until an incursion in the late 1910s and 1920s brought hundreds to the state, including the first known breeders. Numbers declined again in the 1940s, built up again in the 1950s, and thereafter drastically declined to the point of their absence by the mid-1960s. Therefore, the recent incursion was not anomalous but rather follows historical patterns of occurrence, indicating that California is on the fringe of the natural range of the Harris' Hawk, with emigration bringing birds into the state and subsequent population decreases leading again to "extirpation."

KEY WORDS: *Harris' Hawk; Parabuteo unicinctus; Baja California; California; population fluctuations.*

Fluctuaciones poblacionales de *Parabuteo unicinctus* y su reaparición en California

RESUMEN.—El gavilán de harris (*Parabuteo unicinctus*) fue considerado como extirpado de California a mediados de 1960. La mayoría de los avistamientos de los últimos 30 años fueron considerados como aves escapadas o liberadas. La especie ha incursionado en el sur de California y norte de Baja California en los años 90, incluyendo unos 50 individuos y algunos eventos de reproducción locales. Esta incursión es aparentemente una más de las ocurridas a largo plazo por esta especie. Cada una trayendo grandes números de individuos al norte y oeste de su rango establecido en Arizona y Baja California. Aunque por primera vez fue registrado en el borde del estado en 1850, el gavilán de harris no fue reportado en reproducción hasta su incursión en 1910 y 1920 con cientos de individuos incluyendo los primeros registros de reproducción. Los números de individuos declinaron otra vez en 1940, aumentaron en 1950, y declinaron drásticamente hasta considerarlos ausentes en 1960. Por lo tanto, la reciente incursión no es anómala, al contrario, sigue los patrones de ocurrencia indicando que California está en el límite del rango natural del gavilán de harris, con su emigración trayendo aves dentro del estado y la subsecuente declinación la cual conlleva a su extirpación.

[Traducción de César Márquez]

The Harris' Hawk (*Parabuteo unicinctus*) ranges from the southwestern United States southward through Central America to central Chile and central Argentina, with a geographically disjunct population on the Baja California peninsula. In the United States, it occurs from southern Arizona, southeastern New Mexico, and central Texas southward (Fig. 1; American Ornithologists' Union 1998). Its range in Arizona, New Mexico, and Tex-

as has been expanding northward in recent years (Bednarz et al. 1988, Bednarz 1995, Dawson 1998). In California, the Harris' Hawk was found formerly throughout the lower Colorado River Valley and in the Imperial Valley south of the Salton Sea (Grinnell and Miller 1944). By the mid-1950s, it was extirpated from California as a breeder (Remsen 1978, Walton et al. 1988), with the last definite wild bird recorded north of Blythe on 28 November

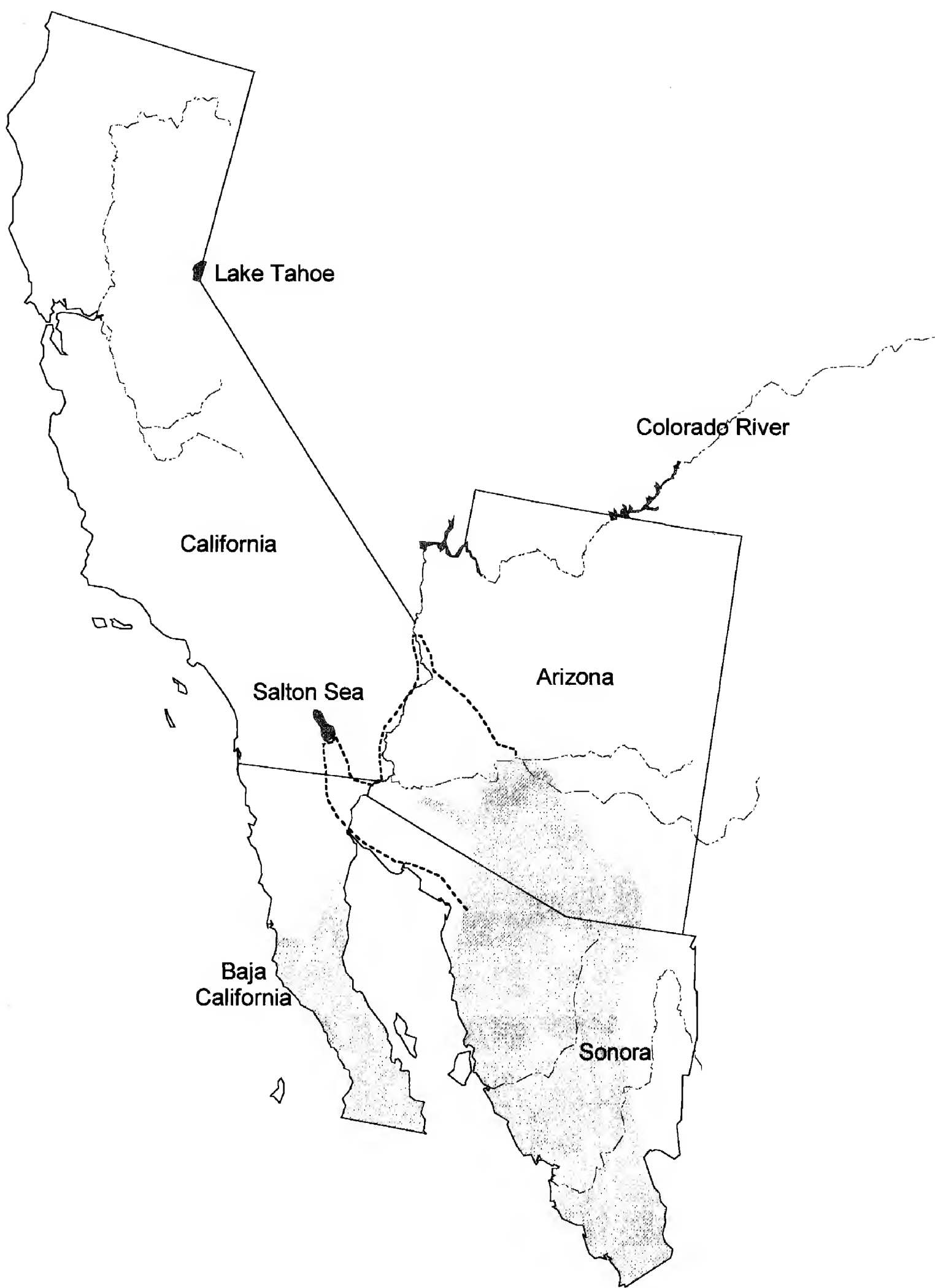


Figure 1. The northwestern portion of the current range (the shaded area) of the Harris' Hawk (*Parabuteo unicinctus*), modified from Bednarz (1995) and Dawson (1998). The dashed line signifies the former westerly limits of its range in southwestern Arizona and southeastern California.

1964 (Garrett and Dunn 1981, Rosenberg et al. 1991).

A reintroduction project for the Harris' Hawk was initiated in California in 1979 by various state, federal, and private groups (Stewart 1979, 1982, Walton et al. 1988). Eight birds were released that year and several more were released each year until 1989, for a total of 222 releases (Linthicum 1989, Linthicum pers. comm.). The first pair nested successfully in 1983, three pairs bred successfully in 1986 (Walton et al. 1988, Rosenberg et al. 1991), and five nested in 1989 (Linthicum 1989, Bednarz 1995). However, it is unlikely that this population is viable, as birds are now infrequently noted (Rosenberg et al. 1991, Patten pers. obs.).

Since the mid-1960s, virtually all recent records of the Harris' Hawk in California are of birds considered to have escaped from falconers (Garrett and Dunn 1981, Unitt 1984). In some cases, birds have been observed with jesses and clearly came from this source. In other cases, there appears to be some tendency for natural occurrence such as sightings of immatures along the Colorado River near Blythe in September (Roberson 1980) and December 1978 (Rosenberg et al. 1991) and at the south end of the Salton Sea on 25 June 1989 (McCaskie 1989). Nevertheless, records of individual birds are perhaps always suspect given that the species remains popular with falconers and rehabilitated birds are occasionally released, as were a few around the Salton Sea in the 1970s and 1980s (Walton et al. 1988). Herein, we document a major increase in sightings beginning in April 1994 that was apparently a natural influx involving nearly 50 individuals throughout southern California and northern Baja California. Further, we hypothesize that such incursions are the rule rather than the exception for the occurrence of this species in California.

METHODS

For the recent incursion, we gathered records and documentation from various field observers (see Acknowledgments) and from files of the California Bird Records Committee. All specific data gathered are on file at the Western Foundation of Vertebrate Zoology (WVZ), Camarillo, California U.S.A. Recent and historical data were gathered from seasonal reports for the Southern Pacific Coast Region published in *Field Notes* (now *North American Birds*), Christmas Bird Counts and specimens at the San Diego Natural History Museum (SDNHM), San Diego, California U.S.A., National Museum of Natural History (USNM), Washington, D.C. U.S.A. and WVZ. We tabulated and mapped these data to obtain an esti-

mate of the magnitude of the incursion and to examine its geographic extent.

THE 1994 INCURSION

Despite an annual "background" escape/release rate throughout California of >3 Harris' Hawks (Bloom pers. comm., Walton pers. comm.), a different phenomenon began 15 April 1994, when J. Rudley, P. Jorgensen, and M. Jorgensen observed three adults together in Borrego Valley. Between 1994–96, at least 34 individuals had been found in southern California (Table 1; McCaskie 1995). The largest groups of birds consisted of at least eight individuals in the Borrego Springs region of the Anza-Borrego Desert and up to five individuals both at the former George Air Force Base near Victorville and at Boulevard (Table 1). During this apparently natural incursion (Bednarz 1995, Massey 1997, Walton pers. comm.), Harris' Hawks were found north of their historical range as far as Victorville in the Mojave Desert, with scattered individuals reported around the Salton Sea and elsewhere (Fig. 2). Additional birds in cismontane valleys at Riverside and in central San Diego County may or may not have been naturally occurring, with individuals far west in coastal Orange County and in the Antelope Valley being particularly suspect given the apparent geographic extent of the influx (Fig. 2). Indeed, the Orange County bird showed signs of being in captivity (Bloom pers. comm., Daniels pers. comm.).

This influx into southern California was concomitant with at least 22 individuals well north of the species' normal range in northern Baja California (Table 2; Rademaker pers. comm., Wurster pers. comm.) and in adjacent northwestern Sonora (Russell and Monson 1998). During this period, Harris' Hawks bred in California at Borrego Springs (Massey 1997), Boulevard (Unitt pers. comm.) and Laguna Dam (McCaskie 1996, Massey 1997), and in northern Baja California at Valle San Telmo (Bloom pers. comm.). Small numbers have persisted in Borrego Valley as recently as 7 March 1999 (Jorgensen pers. comm.) and in Valle San Telmo on 31 January 1999 (Patten pers. obs.).

HISTORICAL TRENDS AND CURRENT STATUS

The historical distribution of the Harris' Hawk in California is not clear. The species was first recorded along the Colorado River on the Arizona side in February 1854 (Kennerly 1859, Swarth 1914), but Elliot Coues never recorded the species

Table 1. California records of the Harris' Hawk (*Parabuteo unicinctus*) from spring 1994 through winter 1996–97 (Fig. 2), arranged chronologically. Birds nested at Boulevard (1994) and Laguna Dam (1996), and exhibited nesting behavior (copulations, carrying sticks and food) at Borrego Valley (1994–95), with immatures observed in 1995. Data are on file with the CBRC.

DATE(S)	LOCATION	MAXIMUM
15 April 1994–January 1999+	San Diego County; Borrego Valley	8
1 June 1994–31 October 1995	San Diego County; Boulevard	5
26 November 1994–29 January 1995	San Diego County; Santee	2
? December 1994	Riverside County; Blythe	1
7–18 December 1994	Imperial County; Westmorland	2
10–12 December 1994	Orange County; Irvine	1
31 December 1994–29 January 1995	Riverside County; n. end Salton Sea	1
2–21 January 1995	San Bernardino County; Victorville	5
27 June–23 July 1995	Riverside County; Riverside	1
6–10 July 1995	San Diego County; Carrizo Canyon	2
3 April 1996	San Diego County; Escondido	1
5 April 1996	San Bernardino County; Vidal Wash	1
25 March–30 December 1996	Los Angeles County; Antelope Valley	1
29 March–April 1996	Imperial County; Laguna Dam	2
31 March 1996	San Diego County; Spring Valley	1

during his extensive surveys of the lower Colorado River Valley in the 1870s and 1880s. It apparently was not recorded at the Colorado River again until August (Stephens 1903) and December 1902 (Wilder 1916), when individuals were noted on both sides of the river. Two specimens collected in the Río Colorado delta of northeastern Baja California bracket these records, a male along the Río Alamo southwest of Pilot Knob on 7 April 1894 (USNM 133726) and a subadult along the Río Hardy on 16 April 1905 (USNM 197921). Thus, a few birds were in the area from the mid-1890s until the early 1900s; however, following the few noted in 1902, the species again went unrecorded in California for a decade. For example, Joseph Grinnell and party did not find the Harris' Hawk during their exhaustive survey of the length of the lower Colorado River Valley 14 February–15 May 1910 (Grinnell 1914). Given the paucity of records through this period, Grinnell (1915) considered the species to be only a “summer visitant” to the Colorado River, based solely on Stephens’ (1903) records.

The Harris' Hawk was not documented as a breeder in southeastern California until the late 1910s, with the first evidence found on 25 July 1916 (Wiley 1917, Bancroft 1920); the first breeding evidence for northeastern Baja California was concomitant (WfVZ 83655). Thus, it is probable that the species had only recently expanded its range into the area. These breeding records were also the

first for the lower Colorado River Valley, as Cooper (1870) made no specific mention of encountering this species. By the mid-1940s, it was “locally common” in California (Grinnell and Miller 1944). There were occasional records of large numbers, although reports of 400–500 between Calexico and Heber, Imperial County, on 22 October 1920 (Chambers 1921) and 250 near Calexico on 28 August 1923 (Chambers 1924) are perhaps best considered tentative given that the species does not travel in large flocks (Bednarz pers. comm.).

The few records of the Harris' Hawk prior to the late 1910s may have involved occasional strays to the west of its established range given its apparent spread into western Arizona. This species “has a reputation for being somewhat nomadic” (Bednarz et al. 1988), with strays being recorded north to Ohio (Earl 1918) and Kansas (Bunker 1919, Snyder 1919), east to Louisiana (Coombs 1892), and west to Utah and Nevada (Palmer 1988). The species has bred opportunistically even at the fringes of its range, including occasional nesting in Kansas (Parmalee and Stephens 1964) and Louisiana (Bailey and Wright 1931). On a smaller scale, groups of Harris' Hawks have been documented to invade and subsequently nest in several regions in southern Arizona east of its normal range (Bednarz 1995). Furthermore, there are two historical records of the Harris' Hawk for coastal San Diego County, California: one collected at Mission Valley

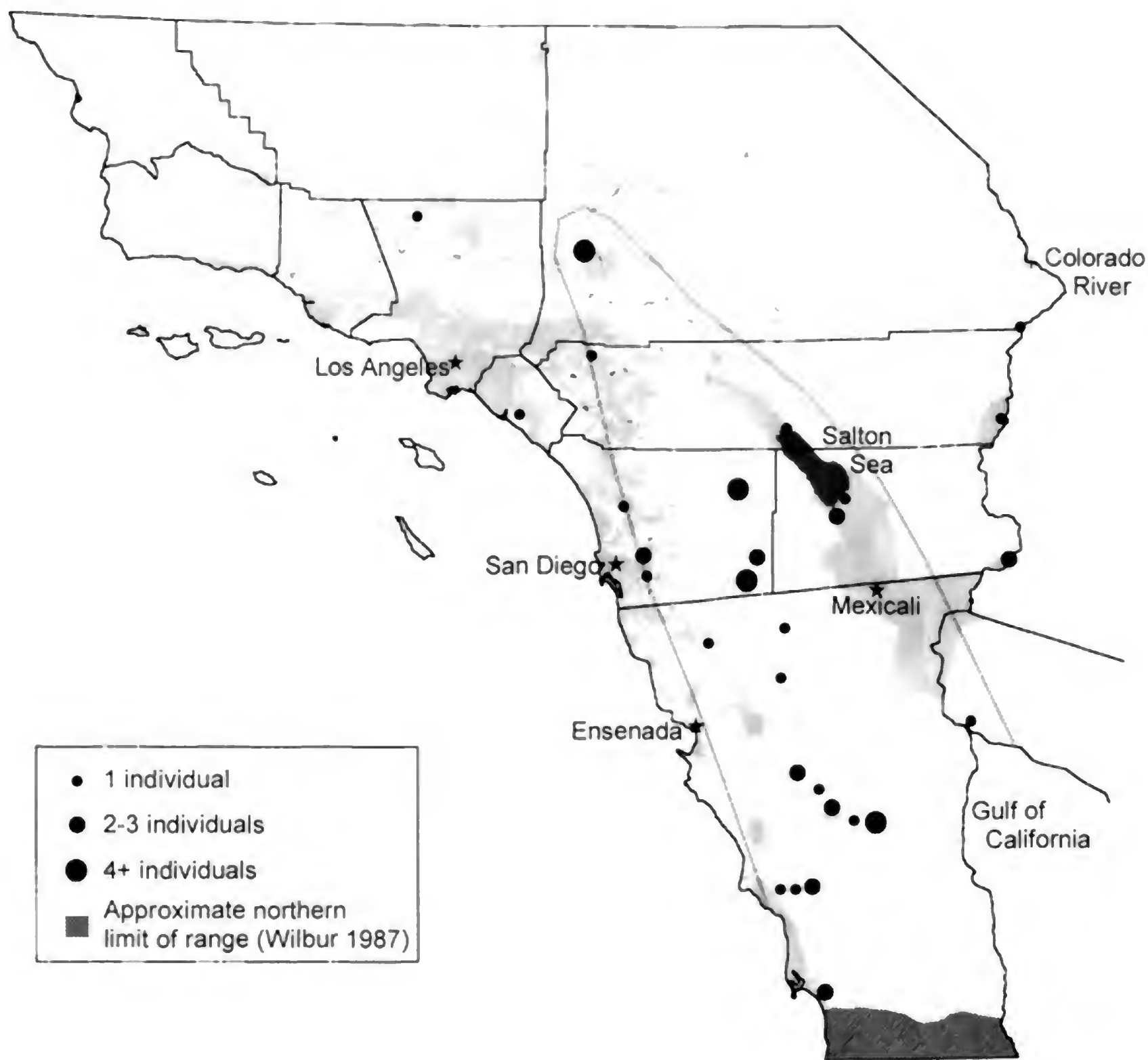


Figure 2. Records of the Harris' Hawk (*Parabuteo unicinctus*) in southern California and northern Baja California since April 1994. The double line identifies the apparent geographic limits of the 1994 incursion. Records within this line are best considered naturally occurring, records falling on the line are debatable, and records well to the west or east are problematic (see text). Shading represents urban/agricultural areas.

on 17 November 1912 (Grey 1913, SDNHM 1842; the second record for California) and one observed at Oceanside from 1–6 November 1942 (Kent 1944).

Although there are no long-term population census data, available data suggest that the Harris' Hawk has undergone four influxes into California during the 20th century (Fig. 3). The first major northwesterly expansion was around the turn of the century when “10–20 [were] in the air at a time” along the lower Colorado River between 1–

3 December 1902 (Wilder 1916). These numbers followed many decades of no records for the lower Colorado River Valley. Elliot Coues never recorded the species during many years of work at Yuma and the species was apparently absent again by 1910 (Grinnell 1914). This dearth was followed by an influx in the late 1910s and early 1920s that was apparently an order of magnitude larger than the incursions of 1902 or 1994, as evidenced by reports of large numbers in the Imperial Valley (Chambers 1921, 1924), a new westerly outpost for the species.

Table 2. Baja California records of the Harris' Hawk (*Parabuteo unicinctus*) north of its normal range from fall 1993 through fall 1995 (Fig. 2). Records are arranged chronologically. Breeding has been documented in the Valle San Telmo, where at least one was still present as of 31 January 1999 (Patten pers. obs.); in addition, an adult was still present at Leyes de Reforma on 7 November 1998 (Erickson pers. obs.). For the sake of completeness we also include one record from this timeframe for the Río Colorado in extreme northwestern Sonora (Russell and Monson 1998). See Methods for data sources (now on file at WFWZ).

DATE(S)	LOCATION	MAXIMUM
5 September 1993–fall 1995+	Valle San Telmo	2
20 February 1994	20 km s. of San Quintin	3
9 April 1994	El Doctor (Sonora)	1
10 April 1994	Valle las Palmas	1
23 April 1994	Laguna Hanson	1
21 May 1994	Campo Christiano	3
21 May 1994–5 March 1995	Valle San Matias	5
30 May 1994	Ejido Sinaloa	1
13 November 1994–fall 1995+	Leyes de Reforma	2
13 November 1994	Valle Trinidad	1
26 March 1995	La Rumorosa	1
10 November 1995	Héroes de la Independencia	1

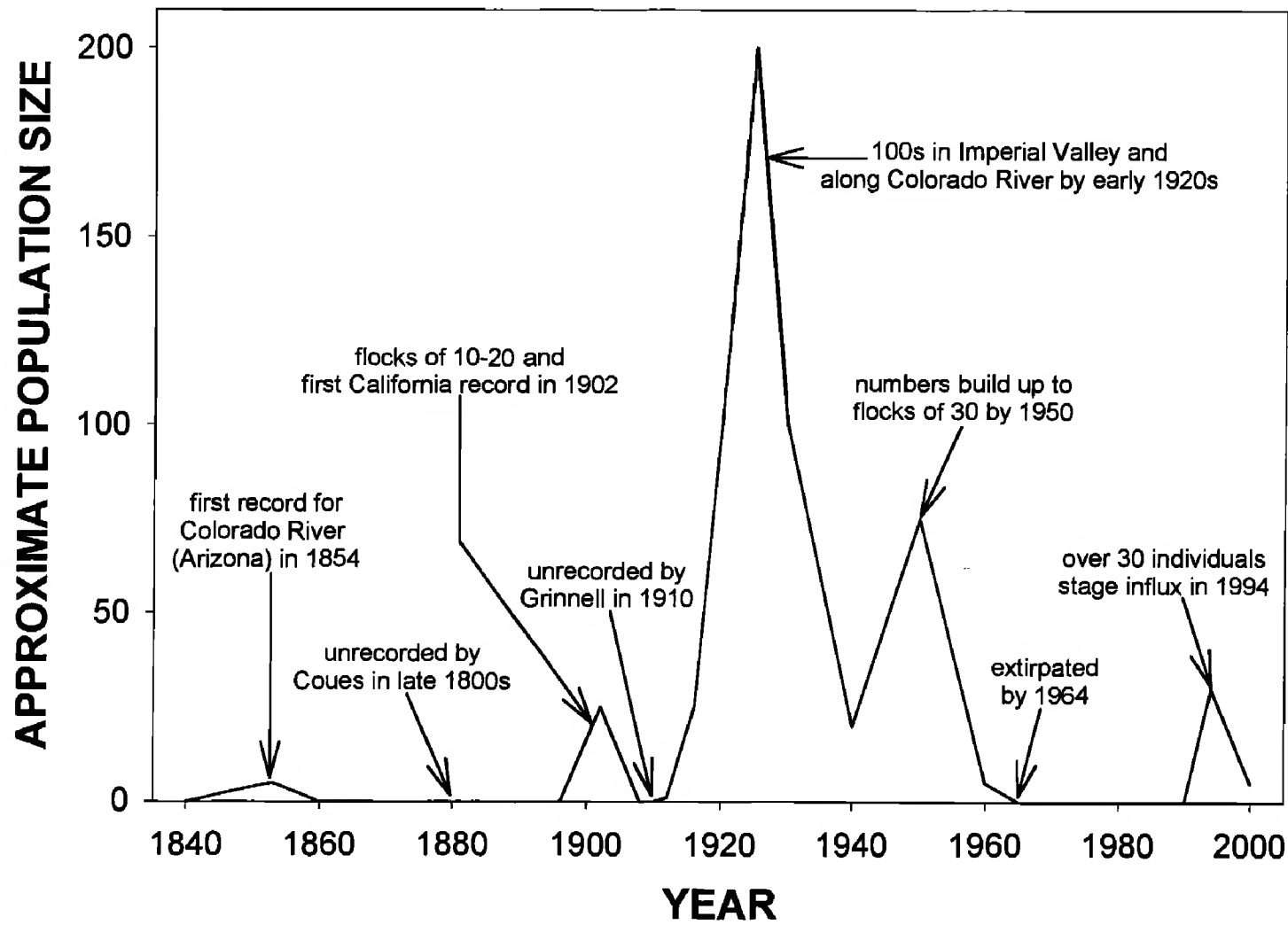


Figure 3. Timeline of the fluctuating occurrence of the Harris' Hawk (*Parabuteo unicinctus*) in California and the lower Colorado River Valley.

There was apparently another influx of Harris' Hawks into California during the late 1940s and early 1950s (Bednarz 1995). During this period numbers again built to double digits (e.g., 30 at Havasu National Wildlife Refuge on 27 December 1950) following two decades of only a few individuals being regularly recorded (Rosenberg et al. 1991).

Two major factors have been implicated in causing the extirpation of this species in California. First, the sport of falconry had an upsurge in popularity in the 1950s, and the Harris' Hawk was and remains a favored bird (White 1988, 1989). Remsen (1978) suggested that nestlings were taken in California until the population was completely depleted, but there is no evidence that falconers ever harvested Harris' Hawks in California (Walton pers. comm.). Instead, birds were harvested in Arizona and Texas and most flown now are from captive breeding. Shooting was undoubtedly common and may also have contributed somewhat to its decline.

Second, habitat loss along the Colorado River from agricultural clearing and water diversion projects was extensive between 1930–60 (Whaley 1986) and similarly occurred during this time in the Imperial Valley (Steere 1952). In addition to direct clearing, erratic water levels led to periodic flooding and desiccation, killing most suitable nest trees. Throughout its range, the Harris' Hawk inhabits savannah-type habitats in arid and semiarid areas, including open woodland, open scrub, mesquite (*Prosopis* spp.) woodland, and riparian woodland bordering open spaces. Trees, especially cottonwoods (*Populus* spp.), or large cacti such as the saguaro (*Carnegiea gigantea*), are used for nesting; however, this species will use utility poles and other artificial structures. In recent years, this species has been steadily increasing its range in southeastern Arizona (Bednarz 1995, Dawson 1998) where it has become more tolerant of human settlements. Indeed, Dawson (1998) noted that "the willingness of Harris' Hawk to nest in urban areas offers some hope of mitigating habitat loss to development," although post-fledging survival of such birds is low (Bednarz pers. comm.).

Perhaps such tolerance for urban setting is a recent advent, for if it were always the case then the Harris' Hawk may have persisted in many areas where it formerly occurred. However, we feel that whereas this urban tolerance may play some small role in the recent incursion into southern Califor-

nia and northern Baja California, it explains neither the magnitude nor the rapidity of the 1994 event. Instead, our investigation supports the hypothesis that the species undergoes periodic population fluctuations that result in rapid range expansions followed by adventitious breeding and, typically, slow range contraction (Millsap 1981, Bednarz et al. 1988). Each expansion-retraction cycle differs in magnitude and may bring individuals into areas where they had not been recorded previously, such as the Mojave Desert. The breeding biology of the Harris' Hawk promotes rapid expansion in numbers when conditions allow. While most nest in spring (March–June), it is able to breed year-round in temperate-climate desert habitats in North America and may produce second and third clutches (Bednarz 1987, 1995). We believe that most birds observed during the 1994 event originated in northern Baja California, where rainfall totals at Ensenada were 140% of average during winter 1991–92 and 168% in 1992–93, but were 90% average in 1993–94 (Mellink pers. comm.). Perhaps two years of favorable conditions allowed for an increase in numbers sufficient to send birds far afield during less favorable conditions in 1993–94, although causes are likely more complex.

In summary, the available evidence suggests that the Harris' Hawk has always been on the fringe of its natural range in California, with occasional irruptive occurrences into the state every few decades. Many stay to breed or linger for significant periods, but eventually numbers decline as appeared to be happening already in the wake of the influx of 1994. As noted above for Louisiana and Kansas, this species is capable of adventitious breeding following a lengthy dispersal. Furthermore, the more general pattern of range expansion and contraction has been documented repeatedly in Arizona and New Mexico (Bednarz 1995, Dawson 1998), although it is perhaps more dramatic in California given that the species may not occur in the state for years at a time.

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THE FOOD HABITS OF SYMPATRIC FOREST-FALCONS DURING THE BREEDING SEASON IN NORTHEASTERN GUATEMALA

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ABSTRACT.—The food habits of Barred (*Micrastur ruficollis*) and Collared Forest-Falcons (*M. semitorquatus*) were studied in Tikal National Park, Guatemala. On a numerical basis for 405 identified prey for Barred Forest-Falcons, lizards (*Anolis* spp., *Ameiva* or *Cnemidophorus* spp., *Laemactus* spp., and *Corytophanes* spp.) were the most numerous prey type comprising 61.5% of the diet. For Collared Forest-Falcons, on a numerical basis of 170 identified prey, mammals represented the greatest proportion at 45.9%. On a biomass basis, lizards (37.3%) and birds (36.8%) were equally important in the diet of Barred Forest-Falcons but, for Collared Forest-Falcons, mammals (47%) and birds (45.4%) were the most important prey. Food-niche overlap was 0.49 between the two forest-falcons and prey that overlapped were mice, rats, bats, birds (*Momotus* spp., *Dendrocincla* spp.), and lizards (*Corytophanes* spp.). The wider food breadth of the Collared Forest-Falcon was probably attributable to the greater diversity of bird species in its diet. The Collared Forest-Falcon is approximately 3 times the size of Barred Forest-Falcons but the mean weight of its prey (MWP) was 10 times greater (\bar{x} = 239 g) than that of Barred Forest-Falcons (\bar{x} = 24 g).

KEY WORDS: *Barred Forest-Falcon*; *Micrastur ruficollis*; *Collared Forest-Falcon*; *Micrastur semitorquatus*; *food habits*; *niche overlap*; *niche breadth*.

Hábitos alimenticios de dos halcones de bosque simpátricos durante la estación reproductiva en el noreste de Guatemala

RESUMEN.—Los hábitos alimenticios de *Micrastur ruficollis* y *Micrastur semitorquatus* fueron estudiados en Parque Nacional Tikal, Guatemala. En una base numérica de 405 presas identificadas para *Micrastur ruficollis*, las lagartijas (*Anolis* spp., *Ameiva* o *Cnemidophorus* spp., *Laemactus* spp., y *Corytophanes* spp.) fueron el tipo de presa más numeroso o sea el 61.5% de la dieta. Para *Micrastur semitorquatus*, en una base numérica de 170 presas identificadas, los mamíferos representaron la proporción mayor con el 45.9%. En relación a la biomasa, las lagartijas (37.3%) y aves (36.8%) fueron igualmente importantes en la dieta de *Micrastur ruficollis*, pero para *Micrastur semitorquatus*, los mamíferos (47%) y aves (45.4%), fueron las presas más importantes. El traslape del nicho alimenticio fue de 0.49 entre los dos halcones de bosque y las presas que se traslaparon fueron ratones, ratas, murciélagos, aves (*Momotus* spp., *Dendrocincla* spp.), y lagartijas (*Corytophanes* spp.). El espectro más amplio de la dieta de *Micrastur semitorquatus* fue probablemente atribuible a la mayor diversidad de especies de aves en su dieta. *Micrastur semitorquatus* es 3 veces el tamaño de *Micrastur ruficollis* pero su peso medio fue 10 veces mayor (\bar{x} = 239g) que el de *Micrastur ruficollis* (\bar{x} = 24 g).

[Traducción de César Márquez]

Neotropical birds of prey are poorly known, especially the forest-dependent species which are inconspicuous in their habits. The secretive forest raptors of the genus *Micrastur* are among the least-studied raptors and most accounts of their diets come from stomach contents of museum specimens or incidental observations (Dickey and van Rossem 1938, Friedmann 1948, Smith 1969, Izawa 1978, Mader 1981, Willis et al. 1983, Mays 1985, Trail 1987, Rappole et al. 1989, Thorstrom et al. 1990). The most detailed account of the food hab-

its of this genus is given by Robinson (1994), but it too is limited to incidental observations.

The Barred Forest-Falcon (*Micrastur ruficollis*) is perhaps the most common raptor in Neotropical forests. It has the widest distribution of any forest-falcon, occurring from southeastern Mexico to northern Argentina, Paraguay, and east through Brazil and the Guianas (Brown and Amadon 1989, del Hoyo et al. 1994). It ranges from humid lowland and foothill forests to higher subtropical and montane forests reaching its limit near 2500 m. In-

formation on the diet of the Barred Forest-Falcon suggests that it feeds mainly on lizards (Thorstrom et al. 1990, Thorstrom 1993, del Hoyo et al. 1994).

The Collared Forest-Falcon (*M. semitorquatus*) also has a broad distribution, ranging from central Mexico to eastern Bolivia, northern Argentina, and Paraguay (Brown and Amadon 1989). It occupies dense primary and secondary forests from sea level to 2500 m. A recent sighting in Texas (Lasley et al. 1994) extended its northern distribution to the southwestern U.S. Food of the Collared Forest-Falcon includes birds, mammals, lizards, snakes, and insects (Brown and Amadon 1989, Thorstrom 1993).

In this paper, I compare the diet of Barred Forest-Falcons and Collared Forest-Falcons based on several years of nest observations of prey deliveries, and direct observations at and away from nests during breeding seasons from 1988–92 in northeastern Guatemala. My objectives were to compare prey frequency and biomass and to assess the amount of overlap in diet among the two species and compare food-niche parameters and differences as potential mechanisms for coexistence of these two forest-falcons.

STUDY AREA AND METHODS

I studied Barred and Collared Forest-Falcons in Tikal National Park, Petén, Guatemala from 1988–92. The park encompasses 576 km² in northeastern Guatemala and its center lies at 17°13'N, 89°36'W. Vegetation in the park is semideciduous tropical forest with lowland rolling hills ranging from 200–450 m elevation.

Schulze and Whitacre (1999) described several forest types that occur along topographical drainage, soil type, and moisture gradients within the park. The two extremes of this forest-type continuum are upland or high-ground forests (tall, semi-evergreen forests on well-drained, shallow soils) and “bajo” forests (low in stature, with open canopy and dense understory, occurring in low-lying sites of deep, clay-rich soils subject to seasonal flooding and drought). Tikal National Park is covered mostly by unbroken primary forest, except for some areas where light selective logging occurred prior to 1969.

The climate has pronounced wet and dry seasons with rains usually beginning in May or June and ending by December. Between 1989–95, monthly precipitation ranged from 1.0 mm in April to 302.5 mm during September with an annual mean rainfall of 1309 mm (pers. obs.). Mean monthly temperatures ranged from a low of 15°C in January to a high of 35°C in May.

The forest and known forest-falcon territories were searched daily from February through August to document nesting activity and potential breeding pairs. Nests of Barred Forest-Falcons were observed primarily from the ground and those of the Collared Forest-Falcon were occasionally observed from tree platforms. Observations

were made using 7–10× binoculars at distances of 25–50 m. During the breeding season, observations of prey items were recorded during prey deliveries and away from nests during radiotracking sessions. All prey was identified to the most accurate taxonomic level possible with the exception of amphibians and insects, which were not identifiable to the species level and were assigned to larger taxonomic groupings. The resulting tabulation produced a total of 37 prey categories for both species. Only observed prey delivered and captured were included in biomass estimates to avoid possible bias from prey found in nests (Snyder and Wiley 1976, Wiley and Wiley 1981, Marti 1987). *Anolis* lizards were separated in small (<20 cm) and large categories (>20 cm).

To estimate mean weight of prey (MWP), I multiplied each prey item by its average weight (Table 1), summed the products and divided the sum by the total number of prey observed. Mammal weights follow Emmons and Feer (1997), bird weights come from Smithe (1966) and Dunning (1993), and reptile weights were taken in the field.

Food-niche breadths (FNB) were calculated using Levins' (1968) equation: $FNB = 1/\sum P_i^2$, where P_i is the proportion of the i th prey category of species j . For comparison among raptors with different number of prey categories, a standardized niche breadth value (FNBs) was also calculated as follows: $FNBs = (FNB - 1)/(n - 1)$, where n is the number of prey categories (Levins 1968). Niche overlap was calculated using Schoener's (1970) index of symmetrical overlap: $overlap = 1 - (1/2)(\sum |P_{ij} - P_{ik}|)$, where P_i is the proportion of the i th prey category for species j and k . Linton et al. (1981) found this overlap formula to be the only index that accurately measures real overlap between 7–85%.

The Collared Forest-Falcon is the largest of the two species with a body mass of 467–511 g for males (Dickey and van Rossem 1938) and 556–750 g for unknown sexes (Haverschmidt 1968). Males I weighed averaged 587 ± 17.6 g (\pm SD, range = 563–605 g, $N = 4$) and females averaged 869 ± 63 g (range = 792–940 g, $N = 6$). Barred Forest-Falcons averaged 167.8 ± 10.6 g (range = 144–184 g, $N = 25$) for males and 233.2 ± 23.9 g (range = 200–322 g, $N = 34$) for females.

RESULTS

Barred Forest-Falcon. I recorded lizards (*Anolis* spp., *Ameiva* spp. or *Cnemidophorus* spp., *Laemactus* spp., and *Corytophanes* spp.), birds (*Momotus* spp., *Aulacorhynchus* spp., *Turdus* spp., *Leptotila* spp., *Dendrocicla* spp., *Thryothorus* spp., and Tyrannidae), amphibians, mammals, snakes, and insects (Blattidae) in the diet of Barred Forest-Falcons during the nesting season.

I observed a total of 600 prey items being delivered to females, nestlings, and fledglings from 1988–92. On a numerical basis, reptiles were the predominant prey comprising 61.5% of the diet (249 prey items), followed by birds 22% (89), insects 8.2% (33), mammals 5.9% (24), and amphibians 2.5% (10) (Fig. 1). Nearly one third (195) of

Table 1. Weights used to estimate prey biomass of Barred and Collared Forest-Falcons at Tikal National Park, Guatemala.

PREY	WEIGHT (g)	SOURCE
Insects		
Blattaria	1.5	This study
Reptiles		
Anolis <20 cm	3.9	This study
Anolis large >20 cm	13.8	This study
Ameiva or Cnemidophorus	25	This study
Laemactus	15	This study
Corytophanes	45	This study
Birds		
Crypturellus	440	Smithe 1966
Penelope	600	Smithe 1966
Crax	500	Smithe 1966
Ortalis	450	Smithe 1966
Agriocharis	3000	Smithe 1966
Odontophorus	300	Smithe 1966
Leptotila	160	Smithe 1966
Ciccaba	240	Smithe 1966
Momotus	133	Dunning 1993
Ramphastos	350	Dunning 1993
Pteroglossus	220	Dunning 1993
Aulacorhynchus	150	Smithe 1966
Melanerpes	81	Dunning 1993
Celeus	85	Dunning 1993
Tyrannidae	15	Smithe 1966
Cyanocorax	200	Dunning 1993
Troglodytidae	15	Smithe 1966
Muscicapidae	75	Smithe 1966
Mammals		
Sciurus small	205	Emmons and Feer 1997
Sciurus large	400	Emmons and Feer 1997
Artibeus	50	Emmons and Feer 1997
Unidentified bat	20	This study
Unidentified mouse (Heteromys)	76	This study, Emmons and Feer 1997
Unidentified rat (Rattus, Oryzomys, Sigmodon)	150	This study, Emmons and Feer 1997

the items were unidentified, especially late in the nestling period, because male forest-falcons flew secretly into their nests without calling their mates to receive prey, and females flew into the nests quickly and directly without vocalizations. It was unlikely, however, that the unidentified prey items differed from those actually identified. The most detailed dietary information was obtained during 1989 when 267 of 380 items delivered to nests were identified. Again, most (64.0%, $N = 171$) were lizards and were represented by 57 small *Anolis* spp., 21 large *Anolis* spp., 28 teiids (most like-

ly *Ameiva* spp. or *Cnemidophorus* spp.), 11 *Laemactus* spp., 5 *Corytophanes* spp., and 49 unidentified lizards. Snakes included 1 coral snake or mimic (*Lampropeltis* sp. or *Micrurus* sp.) and 2 other snakes. Eleven of the 267 identified prey (4%) were frogs (*Rana* spp. and/or *Hyla* spp.). Only 21 arthropods (8 cockroaches and 13 other items including spiders and beetles, 8% of the diet) were identified. Birds contributed 52 prey items (19.5 % of the diet) and included five Blue-crowned Motmots (*Momotus momota*), two flycatchers (Tyrannidae), two Emerald Toucanets (*Aulacorhynchus pra-*

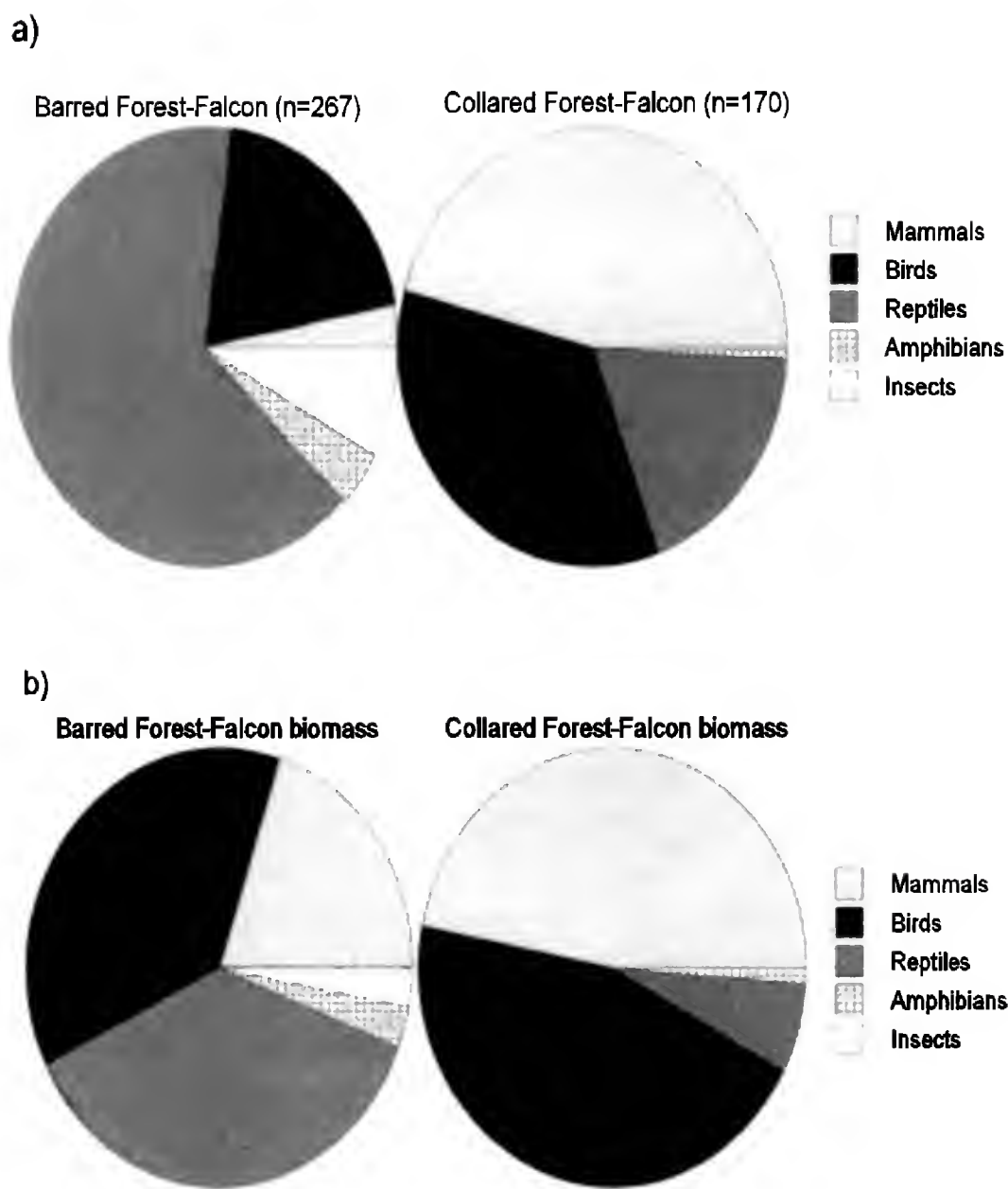


Figure 1. Comparison of the diets of Barred Forest-Falcons and Collared Forest-Falcons as (a) the percent prey of individuals and (b) the biomass composition (% weight of prey individuals).

sinus), one Gray-fronted Dove (*Leptotila rufaxilla*), one woodcreeper (*Dendrocincla* sp.), one Spot-breasted Wren (*Thryothorus maculipectus*), and one Clay-colored Robin (*Turdus grayi*). Birds taken ranged in size from an unidentified warbler (*Dendroica* sp.) at 9 g to a Gray-fronted Dove at 160 g (Smithe 1966, Dunning 1993). The nine mammals I identified represented only 3% of the diet. Among them were seven rodents, one bat, and one other mammal. The rodents were possibly members of the genera *Heteromys* and *Oryzomys*. Snakes accounted for 3 prey items or 1.1% of the diet.

Biomass estimates were made for 267 identified prey items delivered during the 1989 breeding season. On a biomass basis, reptiles (37.3%), birds (36.8%), and mammals (20.2%) comprised 94.3% of the estimated biomass (Fig. 1). Males delivered more prey items and prey biomass than females during the breeding season. Of the 267 identified

prey delivered in 1989, five males brought in 3.8 kg (75.7%) and five females delivered 1.2 kg (24.3%) of the biomass during the breeding season.

Collared Forest-Falcon. I found squirrels (*Sciurus* spp.), bats (*Artibeus* spp.), rats (*Sigmodon* spp.), mice (*Heteromys* spp.), birds (*Crypturellus* spp., *Penelope* spp., *Crax* spp., *Ortalis* spp., *Agriocharis* spp., *Odontophorus* spp., *Leptotila* spp., *Ciccaba* spp., *Momotus* spp., *Ramphastos* spp., *Pteroglossus* spp., *Aulacorhynchus* spp., *Melanerpes* spp., *Celeus* spp., *Cyanocorax* spp., *Dendrocolaptidae*), snakes (*Coluber* sp.), and lizards (*Corytophanes* spp.).

From 1990–92, 222 prey items were delivered to females, nestlings, and fledglings and 170 of these were identified. On a numerical basis, 45.9% were mammals (78 prey items), 34.7% birds (59), 18.8% reptiles (13 lizards and 19 snakes), and 0.6% amphibians (1 frog) (Fig. 1). The 52 unidentified

prey items were presumed to have been similar to those that were identified. In addition, 36 items were given to two fledglings by an extra adult believed to be a male. This male specialized in catching toucans so I calculated the diet of Collared Forest-Falcons both with and without this male's contribution.

Prey of Collared Forest-Falcons ranged in size from a frog estimated at 20 g to an Ocellated Turkey (*Agriocharis ocellata*) weighing about 3 kg. The two largest prey were the adult female turkey and a young Crested Guan (*Penelope purpurascens*). Of the 13 lizards taken, 12 were in species belonging to the genus *Corytophanes*. The 19 snakes I observed were most likely colubrids. The 78 mammals identified included 42 Deppe's squirrels (*Sciurus deppei*; 190–220 g), 11 Yucatan squirrels (*S. yucatanensis*; 420 g), two fruit bats (*Artibeus* spp.), 14 unidentified bats, 7 rat-sized rodents including the hispid cotton rat (*Sigmodon hispidus*), and 2 mice believed to be spiny pocket mice (*Heteromys* spp.). Among the 59 birds identified, the most numerous were Collared Aracari (*Pteroglossus torquatus*, $N = 9$), Plain Chachalaca (*Ortalis vetula*, $N = 7$), Great Curassow (*Crax rubra*, $N = 7$), Keel-billed Toucans (*Ramphastos sulfuratus*, $N = 6$), Ruddy Woodcreepers (*Dendrocincla homochroa*, $N = 4$), Tinamous (*Crypturellus* spp., $N = 3$), and Brown Jays (*Cyanocorax morio*, $N = 3$).

In 1990, a third adult forest-falcon, probably a male, began delivering prey items to two young, 4 wk after they fledged. We observed this adult deliver 36 prey items until 11 weeks after fledging. It appeared to prefer Keel-billed Toucans delivering 27 toucans, two Collared Aracari, two unidentified birds, four squirrels (*S. deppei*), and one unidentified prey item. Sometimes it delivered two Keel-billed Toucans a day. When this contribution was included in the overall diet of Collared Forest-Falcons, the diet was dominated by birds (43.9%, 90 individuals) followed by mammals (40.0%, 82), reptiles (15.6%, 32), and amphibians (0.5%, 1). In terms of biomass, this extra adult delivered 12.6 kg of prey during the post-fledging period.

Biomass estimates were based on the 170 identified prey items delivered during the breeding seasons. On this basis, 47.0% of the prey were mammals, 45.4% birds and 6.5% reptiles (Fig. 1). Squirrels represented 66.7% of the mammalian biomass. Males delivered 11.4 kg (65.7%) and females 5.9 kg (34.3%) of the biomass.

Food-niche Parameters. Lizards, especially *Anolis*

Table 2. Food-niche breadth, dietary overlap, and estimated mean weights (g) of prey (MWP) and of birds (MW) of Barred and Collared Forest-Falcons during the nesting season. All calculations based on prey at the generic or family level. Mean \pm SE (N).

FOOD-NICHE PARAMETERS	BARRED FOREST- FALCON	COLLARED FOREST- FALCON
Total identified prey items	267	170
Mammal species richness	3	6
Bird species richness	7	15
Lizard species richness	5	1
MWP	23.7 \pm 2.5 (267)	238.9 \pm 18.9 (170)
MW birds	62.1 \pm 15.3 (52)	373.4 \pm 49.5 (59)
FNB	7.9	13.8
FNBs	0.33	0.49
Dietary overlap	0.49	

spp., dominated the Barred Forest-Falcon diet and, as a result, it had a narrower niche breadth than did the Collared Forest-Falcon. Collared Forest-Falcons took a higher richness of bird and mammal species (Table 2). The standardized FNB of the Barred Forest-Falcon was lower (0.33) than the Collared Forest-Falcon (0.49). Dietary overlap between the two forest-falcons was 0.49. Estimated MWP captured by Collared Forest-Falcons was significantly heavier than that of Barred Forest-Falcons (Table 2). The larger Collared Forest-Falcon captured larger avian ($\bar{x} = 373.9 \pm 49.5$ g, \pm SE, $N = 59$) and mammalian ($\bar{x} = 179 \pm 12.5$, $N = 78$) prey than did the Barred Forest-Falcon which took mostly lizards ($\bar{x} = 13.8 \pm 0.6$, $N = 122$) and birds ($\bar{x} = 62.1 \pm 4.9$, $N = 52$).

DISCUSSION

Barred and Collared Forest-Falcons are moderately dimorphic with Collared Forest-Falcons 3–4 times larger than Barred Forest-Falcons. Optimal foraging theory predicts that larger predators should have a wider food niche than smaller ones (Schoener 1970). I found this to be true for these two forest-falcons. Collared Forest-Falcons captured a higher proportion of medium-sized mammals, especially squirrels, and they had a greater diversity of birds in their diet giving them a broader food-niche breadth (13.8) compared to Barred

Forest-Falcons (7.9). Barred Forest-Falcons preyed predominantly on lizards, mainly *Anolis* spp., contributing to its narrower food-niche breadth, and birds were of secondary importance in their diet. Collared Forest-Falcons preyed on a wider range of animal sizes, ranging from a small frog (20 g) to large birds (3 kg) whereas Barred Forest-Falcons caught prey ranging in size from insects (1.5 g) to a dove (160 g).

In terms of biomass, Barred Forest-Falcons captured nearly equal proportions of lizards (37.3%) and birds (36.8%) during the breeding season. This was attributed to the smaller mean weight of lizards (13.8 g) vs. the mean weight of birds (93.5 g). Birds were approximately seven times heavier but three times fewer in numbers. Prey biomass of Collared Forest-Falcons was distributed nearly equally between mammals (47%) and birds (45.4%), but the mean weight of birds (368 g) was twice that of mammals (179 g). However, fewer birds (59) than mammals (78) were delivered during the nesting season, contributing to the nearly equal frequency of prey biomass of Collared Forest-Falcons.

The food-niche overlap was relatively high between these two congeners and almost near the competition threshold level of 0.6 which was proposed as biologically significant by Zaret and Rand (1971). Schoener (1984) and Temeles (1985) predicted that similar morphological features of raptors can be found among congeners which affect their hunting ability and food habits. However, Bosakowski and Smith (1992) showed that larger differences in body size limit food overlap below the competition threshold. Thus, while the two forest-falcons exhibited overlap on a few prey species, I suspect that the effect on overall prey availability was probably insignificant. Both species have a broad diet with Barred Forest-Falcons relying more on lizards and Collared Forest-Falcons preying mainly on squirrels.

The Barred Forest-Falcon is dependent on mature forests while the Collared Forest-Falcon occupies mature forests, forest edge, and secondary woodlands and thickets. Both species use a short stay "perch-hunting" technique, a common method found in forest or woodland-adapted species (Kenward 1982, Newton 1986). The higher consumption of avian prey by the Collared Forest-Falcon may be enhanced by its great maneuverability, owing to its long legs and long-arched tail which are morphological adaptations for chasing prey by

foot. Collared Forest-Falcons were observed chasing prey by running on the ground, around tree trunks, and along large branches, whereas Barred Forest-Falcons usually attacked prey by surprise from concealed perches.

The information provided here is limited to observations during the nesting season and may not accurately reflect the overall diet of these two species. There may be seasonal shifts in the diet of these forest-falcons or certain prey types may be taken preferentially due to experience or ability as observed in the extra adult Collared Forest-Falcon that delivered 75% of its prey as Keel-billed Toucans. This particular bird apparently had a special ability or learned behavior for capturing toucans. More information is needed from other regions in the Neotropics and during the nonbreeding season to determine the extent of niche breadth and dietary overlap between these two species.

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A COMPARISON OF RAPTOR DENSITIES AND HABITAT USE IN KANSAS CROPLAND AND RANGELAND ECOSYSTEMS

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ABSTRACT.—We counted raptors on line transects along roads to assess densities, species diversity, and habitat selection of winter raptors between cropland and rangeland habitats in eastern Kansas. We conducted counts every 2 wk between September–March 1994–98. Species diversity indices did not differ between the two habitats ($P = 0.15$). We calculated density estimates and cover type selection for Red-tailed Hawks (*Buteo jamaicensis*), Northern Harriers (*Circus cyaneus*), and American Kestrels (*Falco sparverius*). Red-tailed Hawks and Northern Harrier densities were higher in cropland, while kestrel densities did not differ between the two habitats. All three species across both habitats had a general preference for idleland habitat. We believe three factors could explain the higher raptor densities in cropland: increased prey abundance, increased visibility of prey associated with harvested agriculture fields, and/or a higher relative amount of preferred hunting habitat.

KEY WORDS: *Northern Harrier*; *Circus cyaneus*; *Red-tailed Hawk*; *Buteo jamaicensis*; *American kestrel*; *Falco sparverius*; *cropland*; *cover type selection*; *density*; *line transect*; *rangeland*.

Una comparación de densidades de aves rapaces y uso de hábitat en tierras agrícolas y ecosistemas de pastizales en Kansas

RESUMEN.—Contamos las aves rapaces en transectos lineales a largo de carreteras para evaluar las densidades, la diversidad de especies y la selección de hábitat de las rapaces que pasan el invierno entre las tierras agrícolas y los hábitats de pastizales en el este de Kansas. Hicimos conteos cada 2 semanas entre septiembre y marzo 1994–98. Los índices de diversidad de especies no difirieron entre los dos hábitats ($P = 0.15$). Calculamos las densidades y la selección de cobertura para *Buteo jamaicensis*, *Circus cyaneus*, y *Falco sparverius*. Las densidades de *Buteo jamaicensis* y *Circus cyaneus* fueron mayores en las áreas de cultivos, mientras que las densidades de *Falco sparverius* no difirieron entre los dos hábitats. Las tres especies a lo largo de ambos hábitats tuvieron una preferencia general por el hábitat de tierras sin trabajar. Creemos que tres factores pueden explicar la mayor densidad en tierras cultivadas; aumento de la abundancia de presas, aumento de la visibilidad de presas asociada a las áreas de tierras cosechadas, y/o a un aumento relativo de la cantidad de hábitat de caza.

[Traducción de César Márquez]

Eastern Kansas is the wintering range for 11 species of diurnal raptors. In addition, three species of diurnal raptors migrate through eastern Kansas to wintering and breeding ranges (American Ornithologists' Union 1998). Eastern Kansas Audubon Society Christmas Bird Counts average 41–100 individual falconiform birds per count in 1986 (Johnsgard 1990).

Although there is a large amount of research on the basic winter ecology of many species of raptors (e.g., Craighead and Craighead 1956, Collopy 1973, Bohall and Collopy 1984, Collopy and Bildstein 1987, Temeles and Wellicome 1992, Ardia and Bildstein 1997), little research has examined the effects of different landuse regimes (e.g., agriculture or grazing) on winter raptor ecology.

Consequently, we estimated densities, species diversity, and habitat selection of winter raptors in cropland and rangeland ecosystems in eastern Kansas.

STUDY AREAS

We conducted raptor surveys in both an agricultural and rangeland-dominated landscape in southern Lyon County, Kansas, where there was narrow transition zone between rangeland (western) and cropland (eastern) ecosystems. We selected study areas within this transition zone to ensure that the distance between study areas would reduce confounding climatic differences yet minimize migration between study areas. Both study areas were approximately 2849 ha of private land and separated by 20 km. The cropland study area (CSA) was 3 km west of Hartford, Kansas, and the rangeland study area (RSA) was 7 km west of Olpe, Kansas. Because the study areas were large, we could not spatially replicate our landscapes.

METHODS

The percent coverage of cover types on our study areas was calculated areas using aerial photographs from 1990 and ArcView Geographic Information System (Version 3.1, 1998). The CSA included 49% cropland (e.g., soybeans, sorghum, corn, and winter wheat), 19% native hayland, 16% native tallgrass pasture, 12% idle grassland (e.g., Conservation Reserve Program grasses, grassy waterways, roadsides), and 4% woody cover (e.g., treelines, wooded drainage ways). We identified 65 discrete units of woody cover on CSA, each measuring on average 1.75 ha. Percent coverage of cover types within CSA was similar to agricultural areas within eastern Lyon County (Byram 1996).

The composition of RSA was 72% native tallgrass pasture, 8% hayland, 8% idle grassland, 8% cropland, and 3% woody cover. We identified 28 discrete units of woody cover on RSA, each measuring on average 3.05 ha. As compared to CSA, woody cover units were larger and more fragmented from each other. Percent coverage of cover types within RSA was similar to rangeland areas within the Flint Hills region (Kollmorgan and Simonett 1965), and grazing and burning dominated land use practices (every 1–4 yr). Landowners reported the average annual grazing pressure on RSA was 1 steer/0.81 ha, which was considered overgrazed (Launchbaugh and Owensby 1978, Owensby et al. 1988).

To measure relative diurnal raptor species diversity between study areas, we used the Shannon-Wiener diversity index (Zar 1984) on raw observations of species. By using raw observations, we assumed detectability functions were equal across all species and individuals. We used a two-way ANOVA ($P \leq 0.05$) to compare diversity indices among years and between study areas.

We established a single line transect on roads traversing CSA and RSA (Andersen et al. 1985). An assumption of line transect sampling is that the distribution of observed species is not influenced by the transect lines (Buckland et al. 1993). We feel any violation of this assumption was reduced because roads were generally one lane, unpaved, and had low traffic and telephone and

power poles that could influence raptor abundance were present along 50% of the RSA transect and 55% of the CSA transect (Andersen et al. 1985). Transect length was 31.40 km on CSA and 28.94 km on RSA. We ran transect routes every 2 wk between 15 September–31 March 1994–98. With two observation vehicles, each containing two individuals, we sampled each route on the same day starting approximately 1 hr after sunrise. At each sighting, we stopped the vehicle at approximately a perpendicular angle from where the raptor was first observed perched or flying. We recorded the species, major land use the raptor was occupying, and estimated the distance from car to raptor using rangefinders. We estimated densities with five possible detection functions (HNormal Hermite, Uniform Polynomial, HNormal Cosine, Uniform Cosine, and Hazard Cosine) using program DISTANCE (Laake et al. 1993). The best fit detection function and density was chosen by program DISTANCE ($P \leq 0.05$). We used repeated measures ANOVA to compare density estimates within and among years within study areas and between study areas.

We performed compositional analyses for individual species across all surveys within a given year using log-ratio differences between cover type use and availability (Aebischer et al. 1993). We considered cover type use as the percent of all cover types a species was observed occupying. We considered cover type availability as the percent of all cover types within the study area boundaries. We defined cover type “selection” as the difference between cover type use and availability. We first tested whether all cover type selection was random using Wilk’s lambda statistic ($P \leq 0.05$). We then used 1-sample *t*-tests to rank the selection of cover types (Aebischer et al. 1993). If cover type selection occurred significantly greater than random, we defined the cover type as “preferred.” If cover type selection occurred significantly less than random, we defined the cover type as “avoided.” To compare relative cover type selection between study areas among years, we used 2-way ANOVA.

RESULTS

Species diversity indices did not differ among years within study areas ($F_{3,68} = 1.51$, $P = 0.22$) or between study areas ($F_{1,68} = 3.04$, $P = 0.09$) (Table 1). Due to low sample sizes (mean $N < 10$ per year), we only estimated density and cover type selection for Red-tailed Hawks (*Buteo jamaicensis*, CSA: mean $N = 127$, RSA: mean $N = 127$), Northern Harriers (*Circus cyaneus*, CSA: mean $N = 36$, RSA: mean $N = 20$), and American Kestrels (*Falco sparverius*, CSA: mean $N = 18$, RSA: mean $N = 19$).

Red-tailed Hawk densities did not differ within and among years in both CSA or RSA ($F_{1,6} = 2.79$, $P = 0.15$), so data were pooled within each study area. Densities were three times higher on CSA than on RSA ($F_{1,6} = 14.81$, $P < 0.01$) (Table 2). Habitat use did not differ among years within both study areas ($F_{3,70} < 1.42$, $P > 0.24$) and was pooled within study areas. On both study areas, overall cov-

Table 1. Number of observed diurnal raptors, by species, and species diversity index across the CSA and RSA, Lyon Co., Kansas, winter 1994–95.

COMMON NAME	SCIENTIFIC NAME	CSA					RSA				
		1994– 95	1995– 96	1996– 97	1997– 98	TOTAL	1994– 95	1995– 96	1996– 97	1997– 98	TOTAL
Red-tailed Hawk	<i>Buteo jamaicensis</i>	108	133	130	135	506	63	44	14	25	146
Rough-legged Hawk	<i>Buteo lagopus</i>	0	3	2	1	6	0	3	1	1	5
Swainson's Hawk	<i>Buteo swainsoni</i>	1	0	0	0	1	0	1	0	0	1
Bald Eagle	<i>Haliaeetus leucocephalus</i>	1	1	0	0	2	1	0	0	0	1
Northern Harrier	<i>Circus cyaneus</i>	45	43	29	26	143	43	21	7	10	81
Cooper's Hawk	<i>Accipiter cooperii</i>	1	1	0	0	2	1	4	1	3	9
Sharp-shinned Hawk	<i>Accipiter striatus</i>	1	0	0	0	1	2	0	1	2	5
American Kestrel	<i>Falco sparverius</i>	41	15	4	12	72	28	15	4	27	74
Prairie Falcon	<i>Falco mexicanus</i>	1	3	5	3	12	0	1	3	3	7
Merlin	<i>Falco columbarius</i>	0	0	0	0	0	2	1	0	0	3
Peregrine Falcon	<i>Falco peregrinus</i>	0	0	0	0	0	1	1	0	0	2
Osprey	<i>Pandion haliaetus</i>	0	0	0	1	1	0	0	0	0	0
# Surveys		12	12	10	8	42	12	12	10	8	42
Total species observed		8	7	5	6	10	8	9	7	7	11
Total individuals observed		199	199	170	178	746	141	91	31	71	334
Species Diversity Index		0.350	0.318	0.241	0.307	0.307	0.408	0.385	0.308	0.379	0.377
SE		0.035	0.037	0.041	0.042	0.020	0.036	0.057	0.077	0.041	0.026

Table 2. Winter density estimations of Red-tailed Hawks, Northern Harriers, and American Kestrels in cropland and rangeland study areas, Lyon Co., Kansas, winter 1994-98. Detection functions (Det. Func.) are reported as HC (Hazard Cosine), HNC (Hnormal Cosine), UP (Uniform Polynomial), HNH (HnormalHermite), or UC (Uniform Cosine).

		1994-95			1995-96			1996-97			1997-98			Total		
STUDY AREA	N	N/km ²	(SE)	DET. FUNC.	N	N/km ²	(SE)	DET. FUNC.	N	N/km ²	(SE)	DET. FUNC.	N	N/km ²	(SE)	DET. FUNC.
Red-tailed Hawk																
CSA	108	2.89	(0.91)	HC	133	3.85	(1.51)	HC	130	2.14	(1.03)	HC	135	4.92	(2.22)	HC
RSA	63	1.74	(0.54)	HC	44	0.65	(0.41)	HNC	14	0.47	(0.33)	HC	25	0.67	(0.41)	HC
Northern Harrier																
CSA	45	0.90	(0.37)	HC	43	1.34	(0.83)	HC	29	1.02	(0.37)	HC	26	0.60	(0.17)	HC
RSA	43	0.34	(0.09)	HNC	21	1.03	(0.61)	HC	7	0.07	(0.04)	UP	10	0.30	(0.12)	UP
American Kestrel																
CSA	41	5.14	(2.08)	HC	15	1.97	(0.87)	HC	4	1.28	(0.85)	UP	12	2.60	(0.87)	HC
RSA	28	1.57	(0.79)	HC	15	4.42	(2.36)	HC	4	0.87	(0.47)	UP	27	4.85	(4.12)	HC

er type selection departed from random selection (CSA: $\Lambda < 0.53$, $\chi^2_4 > 44.00$, $P < 0.01$). On CSA, Red-tailed Hawks preferred idle grassland and woody cover ($t_{40} > 2.33$, $P < 0.03$) while avoiding hayland, cropland, and pasture ($t_{40} > 3.81$, $P < 0.01$) (Fig. 1). On RSA, they used pasture equally with availability ($t_{36} = 1.95$, $P = 0.06$), preferred woody cover ($t_{36} = 12.48$, $P < 0.01$), and avoided pasture, hayland, and cropland ($t_{42} > 3.91$, $P < 0.01$) (Fig. 1).

We found Red-tailed Hawks selected hayland and cropland equally between CSA and RSA ($F_{1,70} < 0.47$, $P > 0.50$). However, they selected pasture and woody cover less on RSA than CSA ($F_{1,70} > 5.48$, $P < 0.02$) while they selected idle grassland more on RSA than CSA ($F_{3,70} = 28.34$, $P < 0.01$).

Northern Harrier densities did not differ within or among years in both CSA or RSA ($F_{1,6} = 0.62$, $P = 0.46$), so data were pooled within study areas. Densities were twice as high on CSA than on RSA ($F_{1,6} = 4.22$, $P = 0.09$) (Table 2). Habitat use did not differ among years in either study area ($F_{3,58} < 1.53$, $P > 0.22$) and was pooled within study areas. On CSA overall cover type selection did not depart from random selection (CSA: $\Lambda = 0.96$, $\chi^2_4 = 8.26$, $P < 0.08$) whereas selection on RSA did (RSA: $\Lambda = 0.73$, $\chi^2_4 = 12.87$, $P < 0.01$). On RSA, Northern Harriers used idle grassland equally with its availability ($t_{28} = 1.00$, $P = 0.32$) while avoiding woody cover and hayland ($t_{28} > 2.86$, $P < 0.01$) and preferring pasture and cropland ($t_{28} > 2.58$, $P < 0.02$) (Fig. 1).

We found Northern Harriers selected hayland, idle grassland, woody cover, and cropland equally between CSA and RSA ($F_{1,58} < 3.45$, $P > 0.07$). However, they selected pasture more on RSA than CSA ($F_{1,58} = 9.17$, $P < 0.01$).

American Kestrel densities did not differ within or among years in both CSA or RSA ($F_{1,6} = 1.90$, $P = 0.22$) or between study areas ($F_{1,6} = 0.02$, $P = 0.90$) (Table 2). For kestrels on both study areas, habitat use did not differ among years ($F_{3,41} < 2.71$, $P > 0.06$) and was pooled within study areas. On both study areas, overall cover type selection departed from random selection ($\Lambda < 0.56$, $\chi^2_4 > 24.01$, $P < 0.01$, RSA). On CSA, kestrels used idle grassland and cropland equally with their availability ($t_{24} < 1.33$, $P > 0.20$), preferred woody cover ($t_{24} = 6.48$, $P < 0.01$), and avoided pasture and hayland ($t_{24} > 3.01$, $P < 0.01$) (Fig. 1). On RSA, they used pasture and cropland equally with their availability ($t_{23} < 1.43$, $P > 0.17$), preferred woody

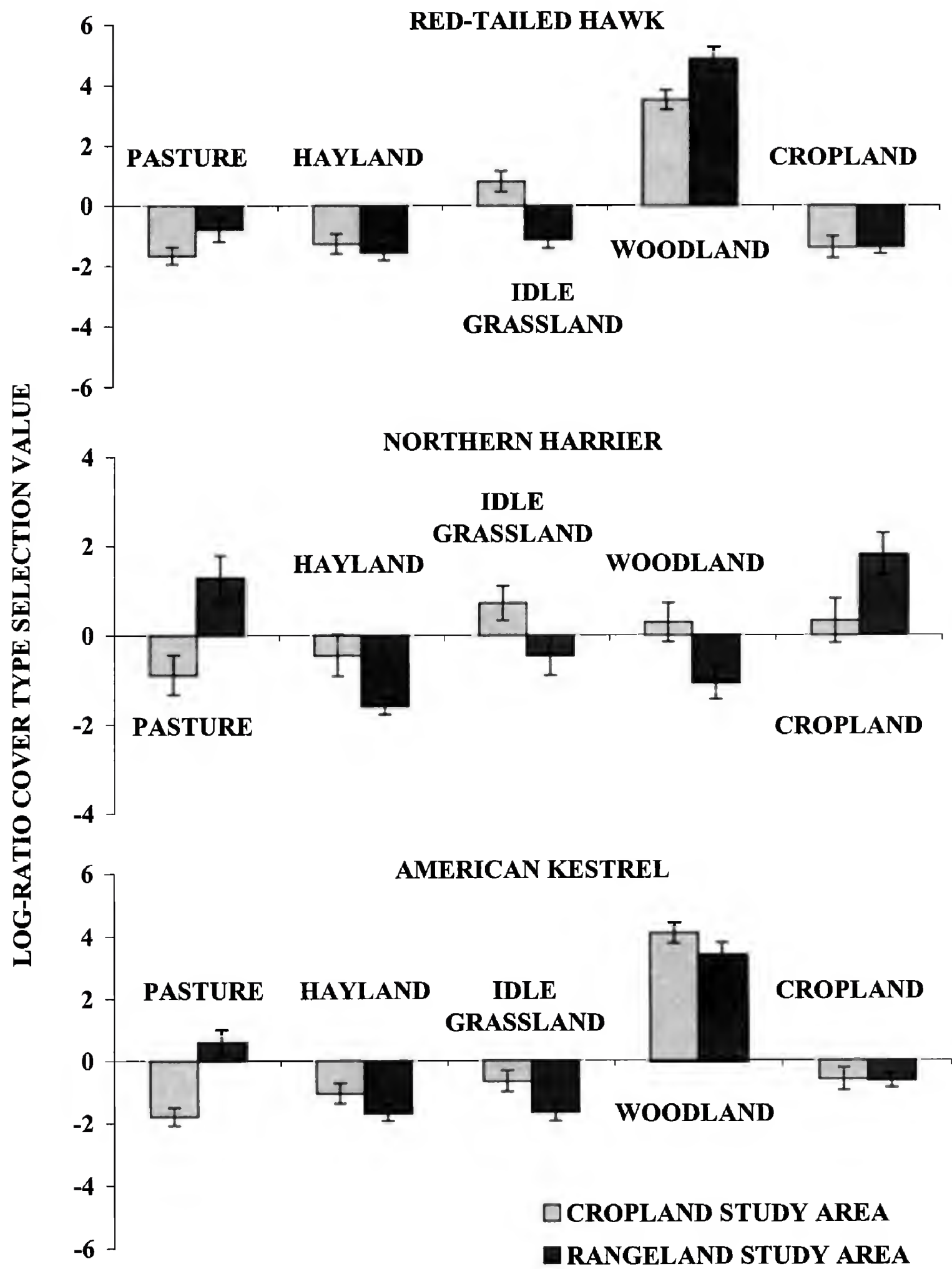


Figure 1. Relative cover type selection given availability (\pm SE) by Red-tailed Hawks, Northern Harriers, and American Kestrels in CSA and RSA, Lyon County, Kansas, 1994–98. Log-ratio cover type selection values above zero indicate relative preference whereas values below zero indicate relative avoidance.

cover ($t_{24} = 5.36$, $P < 0.01$), and avoided hayland and idle grassland ($t_{24} > 14.30$, $P < 0.01$) (Fig. 1).

We found that American Kestrels selected hayland, woody cover, and cropland equally between CSA and RSA ($F_{1,41} < 3.20$, $P > 0.08$). However, they selected pasture more on RSA than CSA ($F_{1,41} = 23.05$, $P < 0.01$) and they selected idle grassland less on RSA than CSA ($F_{1,41} = 4.25$, $P > 0.05$) (Fig. 1).

DISCUSSION

In the four years of our study, we found stable populations of Red-tailed Hawks, Northern Harriers, and American Kestrels. While long-term data (1959–88) from Kansas Christmas Bird Counts (Sauer et al. 1996) suggest that Red-tailed Hawk populations have remained stable, they also found Northern Harriers have declined while American Kestrels have increased.

Our finding that local densities of Red-tailed Hawks and Northern Harriers were higher on CSA is similar to Fitch et al. (1973) who found higher raptor populations in eastern Kansas (similar to CSA) than in the Flint Hills Region (RSA) between 1950–63. We believe several factors could explain higher raptor densities on CSA including prey abundance, prey visibility, and/or the relative amount of preferred hunting habitat.

Relative local prey abundance can affect local raptor densities (Craighead and Craighead 1956, Grant et al. 1991). In a study of Eurasian Kestrels (*Falco tinnunculus*) in cropland and grassland, Village (1989) found kestrel numbers were higher and less variable in cropland ecosystems because of the greater diversity of stable prey populations. Both Red-tailed Hawk and Northern Harrier choice of prey includes small- and medium-sized mammals (mainly rodents), reptiles and small- to medium-sized birds (Preston and Beane 1993, MacWhirter and Bildstein 1996). Additionally, both are known to consume Northern Bobwhite (*Colinus virginianus*) (Errington and Breckinridge 1938, Selleck and Glading 1943). Williams (1996) found that Northern Bobwhite densities were significantly higher on the CSA than on the RSA, potentially indicating a larger prey base on CSA, which in turn could promote a higher abundance of raptors.

Secondly, raptor densities could have been higher on CSA because of the increased visibility of prey associated with harvested agriculture fields. Wakeley (1978) and Bechard (1982) found that selection of hunting sites by Swainson's Hawks (*Buteo*

swainsoni) and Ferruginous Hawks (*Buteo regalis*) was determined more by the presence of prey protective cover than by prey density. Therefore, hawks were present in habitat, such as harvested agriculture, where prey was more vulnerable. However, Preston (1990) and Bildstein (1987) found Red-tailed Hawks and Northern Harriers tended to avoid harvested agriculture and Preston (1990) noted this might be due to lower prey densities in these patches. Because our findings that raptors avoided harvested agriculture generally support Preston (1990) and Bildstein (1987), we question whether this hypothesis could explain higher densities on CSA.

Alternatively, Newton (1979) suggested the shortage of perching sites influence winter raptor density. Relative abundance of perching trees next to open hunting areas have been found to be an important regulating factor for both Red-tailed Hawks and Northern Harriers (Preston and Beane 1993, MacWhirter and Bildstein 1996). Research in Kansas by Cox (1976) and by us indicated the use of woody cover is important habitat for Red-tailed Hawks and Northern Harriers. We believe it is possible that a larger availability of potential hunting areas, associated with woody cover, could have promoted higher densities on CSA.

The abundance of prey and the availability of suitable habitat for roosting and perching affect raptor populations. Consequently, landuse practices can have an impact on raptors. Our results only indicate relationships on our study areas. However, we encourage managers to consider these relationships and address whether they could apply to other agricultural and rangeland systems.

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A REVIEW AND CHECKLIST OF THE PARASITIC MITES (ACARINA) OF THE FALCONIFORMES AND STRIGIFORMES

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ABSTRACT.—Referenced checklists are provided of the 86 species of parasitic feather, quill, respiratory, skin, and nest mites (Acarina) that are known from 116 species of hawks, eagles, falcons, and vultures, and the 91 species of parasitic mites known from 51 species of owls.

KEY WORDS: *Falconiformes; Strigiformes; falcons; hawks; eagles; vultures; owls; parasites; mites; Acarina.*

Un resumen y listado de piojos (Acarina) en Falconiformes y Strigiformes

RESUMEN.—Se provee un listado referenciado de 86 especies de piojos (Acarina) en plumas, quilla, aparato respiratorio, piel y nidos conocidos a partir de 116 especies de gavilanes, águilas, halcones, y buitres y de 91 especies de piojos conocidos a partir de 51 especies de búhos.

[Traducción de César Márquez]

This review summarizes our current knowledge of the host-parasite relationships between parasitic mites and members of the Falconiformes and Strigiformes (Appendices 1 and 2). Over the years, there have been many taxonomic name changes within birds and especially mites, so my review updates old host records to current nomenclature, as well as indicating accidental or misidentified records that should not be regarded as very significant. Nonparasitic nest mites and parasitic mites from prey occur accidentally on raptors, and birds in captivity or specimen bags may pick up mites from other species as well. My review also includes records of some new species, as yet undescribed, which I have found through necropsies of raptors.

There are 21 families of mites that are associated with falconiforms and 17 families associated with owls. Mites inhabit birds' feathers, quills, skin and subcutaneous tissues, respiratory tracts, and nests, and feed on blood, tissue fluid, skin and feather lipids and debris, keratin, fungi, algae, and other mites (Philips 1990, 1993). The mite fauna of most falconiform and strigiform species is completely unknown, but these raptors can host a diverse mite community with as many as eight mite species known from the Black Kite (*Milvus migrans*) and 18 species known from the Long-eared Owl (*Asio otus*). Since mites are so small (0.3–1.5 mm long), they are often overlooked, but raptors that appear parasite-free to the eye can support populations of 15 000 feather mites and 4000 quill mites. Fortu-

nately, most mites on raptors are not very pathogenic and feather mites in particular are usually more commensal, rarely causing harm unless they become extremely abundant.

Feather Mites. There are seven families of falconiform feather mites: Analgidae (*Ancyralges*), Avanzoariidae (*Bonnetella*), Cheylabididae (*Cheylabis*, *Hemicheylabis*), Gabuciniidae (*Aetacarus*, *Aposolenidia*, *Hieracolichus*, *Ramogabucinia*), Kramerellidae (*Pseudogabucinia*), Pterolichidae (*Pseudalloptinus*), and Xolalgidae (*Analloptes*, *Dubininia*). *Ancyralges* occurs only on vultures and *Bonnetella* occurs only on Ospreys (*Pandion haliaetus*). Only a few individuals of *Ancyralges* have been collected, but over 300 *Bonnetella* have been found on an Osprey (Miller et al. 1997). The cheylabidid, gabuciniid, and pterolichid genera which occur on raptors do not occur on other orders of birds, except for *Aetacarus* which includes two species associated with the Otididae. In these genera, species range from monoxenous to polyxenous. *Pseudogabucinia*, *Analloptes*, and *Dubininia* are found on several orders of birds but their falconiform species are restricted to this order. *Aetacarus*, *Hieracolichus*, *Pseudalloptinus*, and *Pseudogabucinia* live on the wings, especially the primaries and upper primary wing coverts. Over 15 000 *Pseudalloptinus* have been found on a single Bald Eagle (*Haliaeetus leucocephalus*). Feather mites feed on feather fragments, lipids secretions, skin debris, and feather fungi, bacteria, and algae. The diet of *Aetacarus* and *Pseudalloptinus* includes fresh-

water diatoms which stick to feathers when birds are in water (Dubinin 1956). In great numbers, feather mites irritate the host with damage resulting from the bird's stress and feather pulling. Vas-yukova and Labutin (1990) found that feather mites occurred on 22% of falconiform birds and 77% of owls in Yakutia.

There are three families of owl feather mites: Kramerellidae (*Dermonoton*, *Kramerella*, and *Petitota*), Psoroptoididae (*Pandahura*), and Xolalgidae (*Glaucalges*). These genera only occur on owls with the exception of one species of *Glaucalges* which occurs on Musophagidae. *Kramerella* species are very host specific, occupy primarily wing feathers, and are often very numerous (thousands) on an individual. Philips (1993) photographed Great Horned Owl (*Bubo virginianus*) alula feathers with *Kramerella* infestations. *Kramerella* is very common on owls and was found on 86% of Eurasian Pygmy-Owls (*Glaucidium passerinum*) in Thuringia (Cerný and Wiesner 1992). *Petitota*, *Pandahura*, and *Glaucalges* species are more polyxenous and typically occur in smaller numbers on a host (Atyeo and Philips 1984). *Dermonoton* also is more polyxenous but population data are lacking.

Quill Mites. There are two families of falconiform quill mites: Ascouracaridae (*Pyonacarus*) and Syringophilidae (*Peristerophila*, undescribed genera). Ascouracarid mites occur on seven orders of birds but *Pyonacarus* is known only from the Black Kite (*Milvus migrans*). These mites eat the medulla of quills. Syringophilid mites use their mouthparts to pierce the quill wall and feed on tissue fluid from the feather follicle. Feather loss and secondary bacterial infection can result. Each genus of Syringophilidae is primarily or exclusively associated with a particular order of birds. *Peristerophila* is a columbiform mite and *P. columbae* is known from pigeons (*Columba livia*) and its occurrence on a Red-tailed Hawk (*Buteo jamaicensis*) (Casto 1976) is unusual and may be accidental. I have found a new genus of syringophilid mite that occurs on five North American accipitrid birds. Trunk and scapular feathers are preferred by falconiform syringophilid mites.

There are three families of owl quill mites: Dermoglyphidae (*Paralges*), Oconnoriidae (*Oconnoria*), and Syringophilidae (*Bubophilus*). Dermoglyphid mites can cause extensive mange because owls use their beaks to dig them out. *Paralges* occurs on several orders of birds, but the undescribed species from owls (Philips 1993) have not been found on other

orders. In owls, *Paralges* colonizes the upper and under trunk feathers but populations over 10 have not yet been found on an individual owl. The family Oconnoriidae is known only from the Philippine Boobook Owl (*Ninox philippensis*) and probably eats the medulla of quills (Gaud et al. 1989). The syringophilid genus *Bubophilus* is known only from the Great Horned Owl (Philips and Norton 1978). Two thousand *Bubophilus* have been found on one bird, inhabiting mainly axillary and nearby wing feathers. Infestations of Great Horned Owl quills with *Paralges* and *Bubophilus* were photographically documented by Philips (1993).

Skin Mites. Skin mites of falconiform birds which live on the skin surface or burrow into the skin include the families Cheyletiellidae, Epidermoptidae (*Microlichus* and *Myialges*), Harpyrhynchidae (*Harpyrhynchus*), and Knemidocoptidae (*Knemidocoptes*). Cheyletiellid mites feed on blood and tissue fluid, and most species are associated with a particular family of birds. *Microlichus* and *Myialges* are also associated with louseflies (Hippoboscidae) and are more fly specific. Their bird host range tends to correspond to that of their fly host. Fertilized *Myialges* females parasitize louseflies and lay their eggs on them, but the other stages of the life cycle are bird parasites. *Microlichus* is phoretic on louseflies and uses them only for a ride to another bird host. *Microlichus* lives in feather bulbs, producing congestion and swelling. These skin mites feed on surface skin debris, keratin, and tissue fluid.

Skin mites of owls which live on the skin surface or burrow into the skin include the families Analgidae (*Strelkoviacarus*), Epidermoptidae (*Microlichus*, *Myialges*, *Passeroptes*), Harpyrhynchidae (*Harpyrhynchus*), and Knemidocoptidae (*Knemidocoptes*). *Strelkoviacarus*, like *Microlichus*, is phoretic on louseflies with a broad avian host range. *Passeroptes* occurs on Passeriformes and Columbiformes as well as owls, but individual species are restricted to one order of bird host.

Harpyrhynchid and knemidocoptid mites burrow into the skin, causing itching and mange. Harpyrhynchid mite species usually have only one avian host species and occur on the calamus at the skin surface and in subcutaneous cysts. Schulz (1990) photographically documented feather loss on the head and neck of a Golden Eagle (*Aquila chrysaetos*) caused by harpyrhynchid mites. This pathology has not been observed in owls. Philips (1993) photographed a harpyrhynchid embedded

in the skin of a Boreal Owl (*Aegolius funereus*). Most knemidocoptid mite species are polyxenous within an order of birds, but those found on owls also occur on other bird orders. Knemidocoptid mites live in the stratum corneum of the skin, causing hyperplasia, hyperkeratosis, and inflammation. They cause scaly encrustations on the beak and claws, known as scaly face and scaly leg disease. This condition in a Great Horned Owl (*Bubo virginianus*) was documented photographically by Schulz et al. (1989) and is common in cage birds, but there is only one record of these mites on falconiform birds (Cooper 1978, 1985).

Transient skin mites of both bird orders include the blood-feeding Dermanyssidae (*Dermanyssus*), Macronyssidae (*Ornithonyssus*), and Laelapidae (*Androlaelaps*), and tissue-fluid feeding Trombiculidae (chiggers). Falconiform chiggers include *Blankaartia*, *Eutrombicula*, *Leptotrombidium*, *Neoschoengastia*, *Odontacarus*, and *Ornithogastia*, while strigiform chiggers include *Blankaartia*, *Euschoengastia*, *Eutrombicula*, *Hyponeocula*, *Leptotrombidium*, *Miyatrombicula*, *Neoschoengastia*, *Odontacarus*, *Ornithogastia*, and *Toritrombicula*. Dermanyssid and macronyssid bird parasites lay eggs on the host or in its nest and chiggers are the parasitic larval stage of a predatory soil mite. All four families usually have relatively low host specificity and can cause dermatitis. Too much blood loss results in energy and weight loss, anemia, and potentially death. *Ornithonyssus* often prefers to feed at the vent. *Dermanyssus* feeds at night. *Dermanyssus* on a Sharp-shinned Hawk (*Accipiter striatus*) was photographed by Philips (1993). Avian *Androlaelaps* species are facultative blood suckers which also prey on other invertebrates and their eggs, on birds, and in their nests. Bird chiggers usually remain attached for three to four days at the thighs, anus, or under the wings.

Subcutaneous Mites. The Hypoderatidae (*Gypsodectes*, *Neottialges*, and *Tytodectes* on hawks, kestrels, and vultures; *Hypodectes*, *Neottialges*, *Neotytodectes*, and *Tytodectes* on owls) are subcutaneous bird mites as nymphs. Nonfeeding adults lay eggs in birds' nests. Nymphs colonize nestlings and adults and live on the surface of breast and abdominal muscles, in fat tissue and, occasionally, in respiratory and circulatory tracts. Lacking a mouth, nutrients are absorbed through the skin. Significant pathological effects from these mites remain unproven, however. Most species of hypoderatid mites have limited host ranges, but a significant number of unusual one-time host

records suggests temporarily successful colonization of other bird hosts in nesting proximity is not uncommon (Pence et al. 1997). This appears to be the case with the record of *Hypodectes propus* from the Burrowing Owl (*Speotyto cunicularia*) and *Neottialges evansi* from the Barn Owl (*Tyto alba*). *H. propus* is associated with pigeons, herons, and egrets and *N. evansi* is a cormorant mite. *Gypsodectes* is known only from vultures; *Neotytodectes* is known only from owls. *Neottialges* is known from four orders of birds, but the species on falconiform birds are monoxenous. *Tytodectes* occurs on owls, falcons, and kingfishers and each species occurs on only one host genus. Several infestations in the Barn Owl were photographically documented by Wurst and Havelka (1997).

Respiratory Mites. Respiratory mites of falconiform birds include the families Ereynetidae (*Boydaiia*, *Speleognathopsis*), Rhinonyssidae (*Falconyssus*, *Ptilonyssus*, *Tinaminyssus*), and Turbinoptidae (*Schoutedenocoptes*). Ereynetid mites feed on mucus deep in the nasal cavity and nonpasserine ereynetid mites are monoxenous or parasitize very few host species. Molted ereynetid mite skins can partially block the nasal cavity. Rhinonyssid mites feed on blood and occupy the anterior portion of the nasal cavity, usually in very small numbers. Each species of these rhinonyssid genera usually has only one or several host species. The genus *Falconyssus* occurs on falconiform and alcedinid birds, while *Ptilonyssus* and *Tinaminyssus* occur on many types of birds. Turbinoptid mites live in the external part of the nares and feed on the corneous skin there. Most turbinoptid species are monoxenous or restricted to one family of birds.

Respiratory mites of owls include the families Cloacaridae (*Pneumophagus*), Ereynetidae (*Astrida*, *Aureliania*, *Neoboydaia*), and Rhinonyssidae (*Rhinoecius*, *Sternostoma*). The Cloacaridae is primarily a family of turtle cloaca mites. One genus is a subcutaneous small mammal parasite and one genus is an owl parasite. *Pneumophagus* is known only from two dozen individuals from the trachea and bronchi of a Great Horned Owl in Michigan (Fain and Smiley 1989). Among the ereynetid mites, *Aureliania* is known only from Barn Owls (*Tyto alba*), *Astrida* is known from owls and Caprimulgiformes, and *Neoboydaia* is known from several orders of birds. *Rhinoecius* is restricted to owls, each species parasitizing one or several owl species. Philips (1993) photographed *Rhinoecius* in the nasal cavity of a Boreal Owl. The genus *Sternostoma* parasitizes many bird orders but most species are restricted to

one or several host species. *Sternostoma tracheacolum*, the canary lung mite, parasitizes passerines and parrots, infiltrating the lung sacs and causing mortality, but the other species remain in the nares and seem to do minimal damage to their hosts. Fleay (1968) suggested that *Kytodites nudus* (the air sac mite, Kytoditidae) may occur in *Ninox strenua*, based on a report by a veterinarian who suspected its presence, but did not find it. This mite feeds on serous secretions in the air sacs of chickens and turkeys and has not been found in owls.

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Appendix 1. A list of the parasitic mites of the Falconiformes.

RAPTOR	MITE	HABITAT	REFERENCES
Family Accipitridae	Epidermoptidae ^a	skin	Herman 1945
Shikra (<i>Accipiter badius</i>)	<i>Knemidocoptes</i> sp.	skin	Cooper 1978, 1985
	<i>Coraciacarus</i> sp. ^b	feathers	McClure and Ratanaworabhan 1971
	<i>Hieracolichus nisi</i>	feathers	Dubinín 1956
Bicolored Hawk (<i>Accipiter bicolor</i>)	<i>Schoutedenocoptes aquilae</i>	nasal cavity	Fain 1977
	mites ^a	skin	Bequaert 1953, Maa 1969
	<i>Aetacarus andrei</i>	feathers	Gaud 1983b
Chestnut-Flanked Sparrowhawk (<i>Accipiter castanilius</i>)	<i>Aetacarus andrei</i>	feathers	Gaud 1983b
Cooper's Hawk (<i>Accipiter cooperii</i>)	<i>Neonyssus</i> sp. ^b	nasal cavity	Peters 1936
Brown Goshawk (<i>Accipiter fasciatus</i>)	Syringophilidae n.g.	quills	Philips, present work
	<i>Speleognathopsis accipitris</i>	nasal cavity	Domrow 1969, Domrow 1991
Northern Goshawk (<i>Accipiter gentilis</i>)	mites ^a	skin	Walter 1989
	<i>Pseudalloptinus aquilinus</i> ^{b,c}	feathers	Nordberg 1936, Niethammer 1938, Dubinín 1956
	<i>Hieracolichus nisi</i>	feathers	Niethammer 1938, Dubinín 1956
	<i>Hieracolichus</i> n. sp.	feathers	Philips, present work
	<i>Neottialges vitzthumi</i>	subcutaneous	Vitzthum 1934, Fain 1967
Slaty-mantled Sparrowhawk (<i>Accipiter luteoschistaceus</i>)	<i>Ornithonyssus sylviarum</i>	skin/nest	Cooper 1978, 1985
Black Goshawk (<i>Accipiter melanoleucus</i>)	mites ^a	skin	Maa 1966
Little Sparrowhawk (<i>Accipiter minullus</i>)	<i>Schoutedenocoptes aquilae</i>	nasal cavity	Fain 1956c, 1957
	<i>Aetaecarus andrei</i>	feathers	Gaud 1983b
Eurasian Sparrowhawk (<i>Accipiter nisus</i>)	<i>Schoutedenocoptes aquilae</i>	nasal cavity	Fain 1956c, 1957
	mites ^a	skin	Newton 1979, Walter 1989
	<i>Cnemidocoptes</i> spp.	skin	Malley and Whitbread 1996
	<i>Dermoglyphus elongatus</i> ^b	quills	Dubinín 1956
	<i>Dubinia accipitrina</i>	feathers	Niethammer 1938
	<i>Hieracolichus nisi</i>	feathers	Canestrini and Kramer 1899, Niethammer 1938, Radford 1953, Dubinín 1956, Vasilev 1961, 1962, Shumilo et al. 1973, Mironov 1997
	<i>Megninia</i> sp. ^b		Niethammer 1938
	<i>Microlichus avus</i> ^a	skin	Walter 1989
	<i>Microlichus</i> sp. ^{a,b}	skin	Ash and Hughes 1952
	<i>Myialges?</i> sp. ^a	skin	Ash and Hughes 1952
Grey Goshawk (<i>Accipiter novaehollandiae</i>)	<i>Myialges uncus</i> ^a	skin	Walter 1989
	<i>Ornithonyssus bursa</i>	skin/nest	Anon. 1963
	mites ^a	skin	Maa 1966, 1969

Appendix 1. Continued.

RAPTOR	MITE	HABITAT	REFERENCES
Ovampo Sparrowhawk (<i>Accipiter ovampensis</i>)	<i>Aposolenidia anomogonima</i>	feathers	Gaud and Atyeo 1974
Sharp-shinned Hawk (<i>Accipiter striatus</i>)	<i>Schoutedenocoptes aquilae</i>	nasal cavity	Fain 1956c, 1957
	mites ^a	skin	Bequaert 1953, Fain 1965, Maa 1969
	<i>Dermanyssus americanus</i>	skin/nest	Philips 1993
	<i>Ornithonyssus iheringi</i>	skin/nest	Dusbábek and Cerný 1971
African Goshawk (<i>Accipiter tacho</i>)	<i>Syringophilae</i> n.g.	quills	Philips, present work
	<i>Aetacarus andrei</i>	feathers	Gaud 1983b
	<i>Myialges asturi</i>	skin	Fain 1965
	<i>Myialges falconis</i>	skin	Fain 1965
Crested Goshawk (<i>Accipiter tri-virgatus</i>)	feather mites	feathers	Maa and Kuo 1965
Besra (<i>Accipiter virgatus</i>)	mites ^a	skin	Maa 1966
	feather mites	feathers	Maa and Kuo 1965
	mites ^a	skin	Maa 1966
	<i>Hieracolichus nisi</i>	feathers	Dubinin 1956
Golden Eagle (<i>Aquila chrysaetos</i>)	<i>Ornithonyssus bursa</i>	skin/nest	McClure and Ratanaworabhan 1971
	<i>Harpyrhynchus</i> sp.	skin	Schulz 1990
	<i>Pseudalloptinus aquilinus</i>	feathers	Trouessart 1884, Lönnfors 1930, Radford 1953, 1958, Dubinin 1956
	<i>Sarcoptes rupicaprae</i> ^b	mammals	Valentincic and Kušej 1989
Greater Spotted Eagle (<i>Aquila clanga</i>)	<i>Pseudalloptinus aquilinus</i>	feathers	Dubinin 1956
Imperial Eagle (<i>Aquila heliaca</i>)	<i>Pseudalloptinus aquilinus</i>	feathers	Dubinin 1956
Lesser Spotted Eagle (<i>Aquila pomarina</i>)	<i>Pseudalloptinus aquilinus</i>	feathers	Radford 1953, 1958, Dubinin 1956
African Tawny-Eagle (<i>Aquila rapax</i>)	<i>Pseudalloptinus aquilinus</i>	feathers	Dubinin 1956
	<i>Pyonacarus</i> sp.	quills	Atyeo pers. comm.
	<i>Schoutedenocoptes aquilae</i>	nasal cavity	Fain 1956c, 1957, Gaud and Till 1961
Verreaux's Eagle (<i>Aquila verreauxii</i>)	<i>Hieracolichus dobyi</i>	feathers	Gaud 1983b
Wahlberg's Eagle (<i>Aquila wahlbergi</i>)	<i>Hieracolichus dobyi</i>	feathers	Gaud 1983b
Grey-lined Hawk (<i>Asturina nitida</i>)	<i>Hemicheylabis praecox</i>	feathers	Trouessart 1885, Gaud and Atyeo 1984
African Baza (<i>Aviceda cuculoides</i>)	<i>Aetacarus avicedae</i>	feathers	Gaud 1983b
	<i>Hieracolichus ostodus</i>	feathers	Gaud 1983b
Pacific Baza (<i>Aviceda subcristata</i>)	<i>Tinaminyssus epileus</i>	nasal cavity	Wilson 1964, 1965
Grasshopper Buzzard (<i>Butastur rufipennis</i>)	<i>Schoutedenocoptes aquilae</i>	nasal cavity	Fain 1956b, 1957
<i>Buteo</i> sp.	<i>Blankaartia allei</i>	skin/nest	Wharton and Fuller 1952
Zone-tailed Hawk (<i>Buteo albonotatus</i>)	<i>Eutrombicula alfreddugesi</i> ^c	skin/nest	Philips 1978
Augur Buzzard (<i>Buteo augur</i>)	<i>Falconyssus buteonis</i>	nasal cavity	Fain 1956b
Common Buzzard (<i>Buteo buteo</i>)	<i>Pseudalloptinus aquilinus</i> ^{b,c}	feathers	Nordberg 1936, Niethammer 1938
	<i>Harpyrhynchus tracheatus</i>	skin	Fritsch 1954
	<i>Hieracolichus nisi</i>	feathers	Canestrini and Kramer 1899, Radford 1953, 1958
	<i>Myialges parv</i> ^a	skin	Büttiker and Cerný 1974
	Prostigmata larva ^a		Büttiker and Cerný 1974
	<i>Pseudogabucinia intermedia</i>	feathers	Gaud 1988

Appendix 1. Continued.

RAPTOR	MITE	HABITAT	REFERENCES
Galapagos Hawk (<i>Buteo galapagoensis</i>)	mites ^a <i>Myialges caulotoon</i> ^a	skin skin	Maa 1969 Harmon et al. 1990, Madden and Harmon 1998
Red-tailed Hawk (<i>Buteo jamaicensis</i>)	mites ^a <i>Aetacarus</i> n. sp. <i>Eutrombicula alfreddugesi</i> <i>Harpyrhynchus</i> sp. <i>Myialges falconis</i> ^a <i>Peristerophila columbae</i> <i>Schoutedenocoptes aquilae</i> Syringophilidae n.g.	skin feathers skin/nest skin skin quills nasal cavity quills	Bequaert 1953, Maa 1969 Philips, present work Loomis 1956 Philips, present work Philips and Fain 1991 Casto 1976 Fain 1956b, 1957 Philips, present work
Red-shouldered Hawk (<i>Buteo lineatus</i>)	<i>Haemogamasus reidi</i> ^b <i>Hieracolichus</i> n. sp. <i>Pseudalloptinus</i> sp.	mammals feathers feathers	Redington 1970 Kurey 1976 Kurey 1976
Roadside Hawk (<i>Buteo magnirostris</i>)	mites ^a <i>Myialges bombycillae</i> ^a <i>Ptilonyssus souzai</i>	skin skin nasal cavity	Maa 1969 Philips and Fain 1991 Pereira and Castro 1949
Broad-winged Hawk (<i>Buteo platypterus</i>)	<i>Hieracolichus</i> n. sp. Syringophilidae n.g.	feathers quills	Philips, present work Philips, present work
Ferruginous Hawk (<i>Buteo regalis</i>)	mites		Bechard and Schmutz 1995
Swainson's Hawk (<i>Buteo swainsoni</i>)	<i>Hieracolichus</i> sp.	feathers	Kurey 1976
Great Black-Hawk (<i>Buteogallus urubitinga</i>)	mites ^a <i>Eutrombicula batatas</i>	skin skin/nest	Maa 1969 Brennan and Yunker 1966
Short-toed Snake Eagle (<i>Circus gallicus</i>)	<i>Hieracolichus nisi</i>	feathers	Canestrini and Kramer 1899, Radford 1953, 1958, Dubinin 1956
Western Marsh-Harrier (<i>Circus aeruginosus</i>)	<i>Pseudalloptes bisubulatus</i> ^b <i>Pseudogabucinia intermedia</i>	feathers feathers	Dubinin 1956 Dubinin 1956
Cinereous Harrier (<i>Circus cinereus</i>)	Ingrassiinae sp. ^a	feathers	Philips and Fain 1991
Northern Harrier (<i>Circus cyaneus</i>)	<i>Pseudogabucinia intermedia</i>	feathers	Dubinin 1956, Cerný 1967, Kurey 1976
Pallid Harrier (<i>Circus macrourus</i>)	mites ^a <i>Aetacarus leptotrichus</i> <i>Myialges macdonaldi</i> ^a	skin feathers skin	Maa 1966 Gaud 1983b Philips and Fain 1991
Montagu's Harrier (<i>Circus pygargus</i>)	<i>Hieracolichus nisi</i>	feathers	Canestrini and Kramer 1899, Nie-thammer 1938, Radford 1953
	<i>Pseudogabucinia intermedia</i>	feathers	Dubinin 1956
Swallow-tailed Kite (<i>Elanoides forficatus</i>)	<i>Aetacarus</i> sp. <i>Macrocheles</i> sp. ^b <i>Ornithonyssus bursa</i>	feathers feathers litter/nest skin/nest	Meyer 1995 Meyer 1995 Meyer 1995
Black-winged Kite (<i>Elanus caeruleus</i>)	<i>Cheylabis latus</i> <i>Falconyssus elani</i> <i>Neottialges elani</i>	feathers nasal cavity subcutaneous	Gaud and Atyeo 1984 Fain 1966a Fain 1969
Australian Black-shouldered Kite (<i>Elanus notatus</i>)	<i>Cheylabis latus</i> <i>Odontacarus australiensis</i> <i>Ornithonyssus bursa</i>	feathers skin/nest skin/nest	Gaud 1983a Domrow 1966, 1991 Domrow 1966
Palm-nut Vulture (<i>Gypohierax angolensis</i>)	mites ^a <i>Aetacarus hyalothrix</i>	skin feathers	Maa 1966 Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1983b
	<i>Hieracolichus orthochaetus</i>	feathers	Gaud and Mouchet 1959b, Gaud 1983b
	<i>Myialges</i> n. sp. ^a <i>Pseudalloptinus africanus</i> <i>Pseudalloptinus odontopus</i>	skin feathers feathers	Philips and Fain 1991 Gaud 1988 Gaud and Till 1961, Gaud 1988

Appendix 1. Continued.

RAPTOR	MITES	HABITAT	REFERENCES
White-backed Vulture (<i>Gyps africanus</i>)	<i>Ancyralges cometus</i>	feathers	Gaud 1966, 1988
	<i>Hemicheylabis sikyonemus</i>	feathers	Gaud 1988
	<i>Hieracoliclus africanus</i>	feathers	Guad and Mouchet 1959b, Gaud and Till 1961, Gaud 1983b
Cape Griffon (<i>Gyps coprotheres</i>)	<i>Gypsodectes verrucosus</i> ^c	subcutaneous	Fain 1984
	<i>Androlaelaps patersoni</i>	skin/nest	Zumpt and Till 1956, Till 1963
	<i>Ramogabucinia doleosikya</i>	feathers	Gaud and Atyeo 1974, Gaud 1983b
Eurasian Griffon (<i>Gyps fulvus</i>)	<i>Gypsodectes vulturis</i>	subcutaneous	Dubinina 1953, 1956, Fain 1967
	<i>Pseudaloptinus aquilinus</i>	feathers	Radford 1953, 1958
White-tailed Eagle (<i>Haliaeetus albicilla</i>)	<i>Aetacus phylloproctus</i>	feathers	Dubinina 1956
	<i>Megninia picimajoris</i> ^b		Niethammer 1938
	<i>Pseudaloptinus aquilinus</i>	feathers	Dubinina 1956, Vasilev 1961
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	<i>Pterolichus obtusus</i> ^b	feathers	Niethammer 1938
	Analgesidae ^b		Spencer 1941
	<i>Pseudaloptinus aquilinus</i>	feathers	Dubinina 1956, Vasilev 1961
White-bellied Fish-Eagle (<i>Haliaeetus leucogaster</i>)	Syringophilidae n.g.	quills	Philips, present work
	<i>Aetacus phylloproctus</i>	feathers	Canestrini and Kramer 1899, Gaud and Petitot 1948b, Radford 1953, 1958, Gaud and Atyeo 1974
Pallas's Sea-Eagle (<i>Haliaeetus leucoryphus</i>)	<i>Pseudaloptinus odontopus</i>	feathers	Gaud and Till 1961, Gaud 1988
	<i>Aetacus phylloproctus</i>	feathers	Dubinina 1956
	<i>Pseudaloptinus aquilinus</i>	feathers	Dubinina 1956, Vasilev 1961
Steller's Sea-Eagle (<i>Haliaeetus pelagicus</i>)	<i>Pseudaloptinus odontopus</i>	feathers	Gaud and Till 1961, Gaud 1988
	<i>Aetacus phylloproctus</i>	feathers	Dubinina 1956
	<i>Pseudaloptinus aquilinus</i>	feathers	Dubinina 1956, Vasilev 1961
Solomon Fish-Eagle (<i>Haliaeetus sanfordi</i>)	<i>Ornithogastia riversi</i>	skin/nest	Wharton and Hardcastle 1946, Goff 1979
	<i>Pseudaloptinus odontopus</i>	feathers	Gaud and Till 1961, Gaud 1988
African Fish-Eagle (<i>Haliaeetus vocifer</i>)	<i>Aetacus puylaerti</i>	feathers	Gaud 1983b
	<i>Hemifreyana marginata</i> ^b	feathers	Gaud and Till 1961
	<i>Hieracoliclus dobyi</i>	feathers	Gaud and Mouchet 1959b
Madagascar Fish-Eagle (<i>Haliaeetus vociferoides</i>)	<i>Pseudaloptinus aquilinus</i>	feathers	Gaud 1988
	<i>Aetacus</i> sp.	feathers	Aty eo pers. comm.
Brahminy Kite (<i>Haliastur indus</i>)	<i>Aetacus haliasturi</i>	feathers	Mégnin and Trouessart 1884d, Radford 1953, 1958, Dubinina 1956
	mites ^a	skin	Maa 1969
	<i>Pseudaloptinus milvulinus</i>	feathers	Radford 1953, 1958, Dubinina 1956
Harpy Eagle (<i>Harpia harpyja</i>)			
	<i>Hieracoliclus hirundo</i>	feathers	Radford 1953, 1958
Solitary Eagle (<i>Harpyhaliaetus solitarius</i>)	<i>Temnalges</i> sp. ^{a,b}	feathers	Philips and Fain 1991
Ayres's Hawk-Eagle (<i>Hieraaetus ayresii</i>)	<i>Aetacus eurychaetus</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1983b
Bonelli's Eagle (<i>Hieraaetus fasciatus</i>)	<i>Hieracoliclus orthochaetus</i>	feathers	Gaud and Till 1961
	<i>Pseudaloptinus aquilinus</i>	feathers	Gaud 1983b
Booted Eagle (<i>Hieraaetus pennatus</i>)	hypopus mites	skin	Hamerton 1941
	<i>Pseudaloptinus aquilinus</i>	feathers	Dubinina 1956
Grey-headed Fish-Eagle (<i>Ichthyophaga ichthyaetus</i>)	<i>Aetacus phylloproctus</i>	feathers	Radford 1958
Mississippi Kite (<i>Ictinia mississippiensis</i>)	<i>Aetacus</i> sp.	feathers	Kurey 1976

Appendix 1. Continued.

RAPTOR	MITE	HABITAT	REFERENCES
Lizard Buzzard (<i>Kaupifalco monogrammicus</i>)	<i>Aetacarus andrei</i> <i>Myialges anchora</i> ^a <i>Schoutedenocoptes aquilae</i>	feathers skin nasal cavity	Gaud 1983b Fain 1965 Fain 1959a
White Hawk (<i>Leucopternis albi-collis</i>)	<i>Temnalges</i> sp. ^{a,b}	feathers	Philips and Fain 1991
Long-crested Eagle (<i>Lophaetus occipitalis</i>)	<i>Falconyssus buteonis</i> <i>Pseudalloptinus milvulinus</i> <i>Pseudogabucinia intermedia</i>	nasal cavity feathers feathers	Fain 1956b Gaud and Till 1961, Gaud 1988 Gaud 1988
Bat Hawk (<i>Macheiramphus alcinus</i>)	mites ^a <i>Myialges macdonaldr</i> ^a	skin skin	Maa 1966 Philips and Fain 1991
Gabar Goshawk (<i>Melierax gabar</i>)	<i>Schoutedenocoptes aquilae</i>	nasal cavity	Fain 1956b, 1957
Dark Chanting-Goshawk (<i>Melixerax metabates</i>)	<i>Aposolenidia anomogonima</i>	feathers	Gaud and Atyeo 1974
Black Kite (<i>Milvus migrans</i>)	<i>Hemicheylabis</i> sp. <i>Aetacarus hyalothrix</i>	feathers feathers	Atyeo pers. comm. Gaud and Mouchet 1959b, Gaud and Till 1961
	<i>Aetacarus milvi</i> <i>Hieracolichus nisi</i> <i>Pseudalloptinus milvulinus</i> <i>Pyonacarus polysarcus</i> <i>Schoutedenocoptes aquilae</i> <i>Tinaminyssus columbae</i>	feathers feathers feathers feathers feathers feathers	Gaud 1983b, D'Souza et al. 1986 Dubinin 1956 Dubinin 1956 Gaud and Atyeo 1976, Gaud 1988 Fain 1956b, 1957 Fain 1957
Red Kite (<i>Milvus milvus</i>)	<i>Pseudalloptinus milvulinus</i>	feathers	Trouessart 1884, Radford 1953, 1958, Dubinin 1956
Hooded Vulture (<i>Necrosyrtes monachus</i>)	<i>Hemicheylabis sikyonemus</i> <i>Hieracolichus monachi</i>	feathers feathers	Gaud 1988 Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1983b
	<i>Pseudalloptinus glossocercus</i> <i>Ramogabucinia furciset</i>	feathers feathers	Gaud 1988 Gaud 1983b
Osprey (<i>Pandion haliaetus</i>)	mites <i>Analloptes buettikeri</i> <i>Analloptes</i> sp. <i>Bonnetella fusca</i>	skin feathers feathers feathers	Bequaert 1953 Mironov 1997 Gaud and Atyeo 1979, Gaud 1983a, Miller et al. 1997 Buchholz 1869, Canestrini and Kramer 1899, Lönnfors 1930, Niethammer 1938, Spencer 1941, Mrciak and Brander 1967, McClure and Ratanaworabhan 1971, Kurey 1976, Gaud 1983a, Mironov 1991, 1997, Miller et al. 1997
Harris' Hawk (<i>Parabuteo unicinctus</i>)	<i>Myialges caulotoon</i> ^a <i>Neoschoengastia americana</i> <i>Pseudalloptinus</i> sp.	skin skin/nest feathers	Philips and Fain 1991 Loomis and Crossley 1963 Atyeo pers. comm.
European Honey-Buzzard (<i>Per-nis apivorus</i>)	feather mites <i>Hieracolichus nisi</i> <i>Hieracolichus ramosus</i>	feathers feathers feathers	Maa and Kuo 1965 Canestrini and Kramer 1899, Nie-thammer 1938, Radford 1953 Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1983b
African Harrier-Hawk (<i>Polyboroides typus</i>)	<i>Hieracolichus similis</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1983b
Martial Eagle (<i>Polemaetus bellicosus</i>)	<i>Hieracolichus dobyi</i> <i>Pseudalloptinus aquilinus</i>	feathers feathers	Gaud 1983b
White-backed Vulture (<i>Pseudogyps africanus</i>)	<i>Dermanyssus gallinae</i>	skin/nest	

Appendix 1. Continued.

RAPTOR	MITE	HABITAT	REFERENCES
Snail Kite (<i>Rostrhamus sociabilis</i>)	<i>Ornithonyssus bursa</i>	skin/nest	Philips et al. 1976, Sykes and Forrester 1983, Sykes et al. 1995
Crested Serpent-Eagle (<i>Spilornis cheela</i>)	<i>Coraciacarus cucul</i> ^b	feathers	Radford 1958
Changeable Hawk-Eagle (<i>Spi-zaetus cirrhatus</i>)	<i>Coraciacarus</i> sp. ^b	feathers	McClure and Ratanaworabhan 1971
Crowned Hawk-Eagle (<i>Stephanoaetus coronatus</i>)	<i>Aetacarus hyalothrix</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961
	<i>Hieracolichus dobyi</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1983b
	<i>Pseudalloptinus odontopus</i>	feathers	Gaud and Till 1961, Gaud 1988
Bateleur (<i>Terathopius ecaudatus</i>)	<i>Hieracolichus dobyi</i>	feathers	Gaud 1983b
White-headed Vulture (<i>Trigonoceps occipitalis</i>)	<i>Hieracolichus monachi</i>	feathers	Gaud 1983b
Long-tailed Hawk (<i>Urotriorchis macrourus</i>)	<i>Myialges caulotoon</i> ^a	skin	Philips and Fain 1991
	<i>Pseudogabucinia</i> sp. ^a	feathers	Philips and Fain 1991
Family Cathartidae			
Turkey Vulture (<i>Cathartes aura</i>)	mites ^a	skin	Bequaert 1953, Maa 1969
	<i>Ancyralges</i> sp.	feathers	Kurey 1976
	<i>Hieracolichus</i> sp.	feathers	Peters 1936, Kurey 1976
	<i>Ornithonyssus bursa</i>	skin/nest	Peters 1936
	<i>Ptilonyssus ohioensis</i>	nasal cavity	Fain and Johnston 1966
Lesser Yellow-headed Vulture (<i>Cathartes burrovianus</i>)	<i>Hieracolichus</i> sp.	feathers	Atyeo pers. comm.
Black Vulture (<i>Coragyps atratus</i>)	mites ^a	skin	Bequaert 1953
	<i>Eutrombicula alfreddugesi</i>	skin/nest	Wharton and Fuller 1952
	<i>Hieracolichus</i> sp.	feathers	Kurey 1976
	<i>Histiogaster</i> ^{a,b}	trees	Philips and Fain 1991
	<i>Ptilonyssus donatoi</i>	nasal cavity	Pereira and Castro 1949
	<i>Sancassania</i> sp. ^{a,b}	litter/nest	Philips and Fain 1991
Andean Condor (<i>Vultur gryphus</i>)	<i>Hieracolichus</i> spp.	feathers	Atyeo pers. comm.
Family Falconidae			
<i>Falco</i> sp.	mites ^a	skin	Bequaert 1953, Fain 1965
	<i>Ptilonyssus cerchneis</i>	nasal cavity	Bregetova 1964
Saker/Peregrine hybrids	<i>Dermanyssus gallinae</i>	skin/nest	Malley and Whitbread 1996
Grey Kestrel (<i>Falco ardosiaceus</i>)	<i>Pseudalloptes falconis</i>	feathers	Gaud 1983a
Brown Falcon (<i>Falco berigora</i>)	<i>Boydaiia falconis</i>	nasal cavity	Domrow 1991
	<i>Leptotrombidium nissani</i>	skin/nest	Domrow and Lester 1985
	<i>Ptilonyssus cerchneis</i>	nasal cavity	Domrow 1965, 1967, 1969
	<i>Odontacarus nadchatrami</i>	skin/nest	Goff 1979
Lanner Falcon (<i>Falco biarmicus</i>)	<i>Pseudalloptes falconis</i>	feathers	Gaud 1983a
	<i>Pseudogabucinia microdisca</i> ^b	feathers	Gaud 1983a
Australian Kestrel (<i>Falco cenchroides</i>)	<i>Leptotrombidium nissani</i>	skin/nest	Domrow 1974, Domrow and Lester 1985
	<i>Odontacarus australiensis</i>	skin/nest	Domrow 1966, 1991
	<i>Ornithonyssus bursa</i>	skin/nest	Domrow 1977
	<i>Ornithonyssus sylviarum</i>	skin/nest	Domrow 1987
	<i>Ptilonyssus cerchneis</i>	nasal cavity	Domrow 1965, 1967, 1969
Red-necked Falcon (<i>Falco chicquera</i>)	<i>Pseudalloptes falconis</i>	feathers	Gaud 1983a

Appendix 1. Continued.

RAPTOR	MITE	HABITAT	REFERENCES
Saker Falcon (<i>Falco cherrug</i>)	<i>Dermanyssus</i> sp.	skin/nest	Wheeldon pers. comm.
Merlin (<i>Falco columbarius</i>)	<i>Dubininia accipitrina</i>	feathers	Vasilev 1958, Cerný 1967, Gaud 1980, 1983a
	Gabuciniidae	feathers	Kurey 1976
	<i>Hieracolichus</i> sp.	feathers	Gaud 1983a
	<i>Microlichus avus</i> ^a	skin	Hill et al. 1967
African Hobby (<i>Falco cuvieri</i>)	<i>Boydaia falconis</i>	nasal cavity	Fain 1956a
Eleonora's Falcon (<i>Falco eleonora</i>)	Acarina sp.		Wink et al. 1979
	<i>Kramerella major</i> ^b	feathers	Mégnin and Trouessart 1884a
	<i>Pseudogabucinia intermedia</i>	feathers	Dubinin 1953, 1956, Radford 1958, Gaud 1983a
Lesser Kestrel (<i>Falco naumanni</i>)	<i>Dubininia accipitrina</i>	feathers	Gaud and Petitot 1948a, Gaud 1958, 1983a
Peregrine Falcon (<i>Falco peregrinus</i>)	<i>Aetacarus</i> ? sp.	feathers	Kurey 1976
	<i>Glaucalges attenuatus</i> ^a		Niethammer 1938
	<i>Hieracolichus nisi</i>	feathers	Dubinin 1956, Cerný 1967, Gaud 1983a
	<i>Pandalura strigisoti</i> ^b		Niethammer 1938
	<i>Pseudallophtinus</i> sp.	feathers	Kurey 1976, Gaud 1983a
	<i>Pseudogabucinia intermedia</i> ^c	feathers	Nordberg 1936, Niethammer 1938, Dubinin 1953, Radford 1958, Gaud 1983a
Oriental Hobby (<i>Falco severus</i>)	<i>Ornithogastia riversi</i>	skin/nest	Wharton and Hardcastle 1946, Goff 1980
American Kestrel (<i>Falco sparverius</i>)	<i>Dubininia</i> sp. ^c	feathers	Philips 1990
	<i>Tytodectes cerchneis</i> ^c	subcutaneous	Philips and Dindal 1979, Philips 1990
	<i>Blankaartia velascoi</i>	skin/nest	Wharton and Fuller 1952
	<i>Boydaia falconis</i>	nasal cavity	Pence and Casto 1976
	<i>Ptilonyssus cerchneis</i>	nasal cavity	Strandtmann 1962
Eurasian Hobby (<i>Falco subbuteo</i>)	<i>Microlichus falco</i>	skin	Fain and Gaud 1972, Fain et al. 1987, Fain and Grootaert 1996
	<i>Neottialges heteropus</i>	subcutaneous	Giebel 1861, 1871, Fain 1967
	<i>Pseudallophtinus minor</i>	feathers	Mégnin and Trouessart 1884b, Canestrini and Kramer 1899, Dubinin 1956, Gaud 1983a
	<i>Pseudogabucinia intermedia</i>	skin	Niethammer 1938, Radford 1953, 1958, Vasilev 1961, Gaud 1983a
Common Kestrel (<i>Falco tinnunculus</i>)	<i>Boydaia falconis</i>	nasal cavity	Fain 1963a
	<i>Cheyletiella</i> sp. ^d		Niethammer 1938
	<i>Dubininia accipitrina</i>	feathers	Trouessart 1885, Canestrini and Kramer 1899, Niethammer 1938, Radford 1953, 1958, Gaud 1958, 1983a
	<i>Megninia</i> sp. ^b		Niethammer 1938
	<i>Myialges</i> sp. nr. <i>pari</i> ^a	skin	Philips and Fain 1991
	<i>Protolichus lunula</i> ^b	feathers	Vasilev 1961
	<i>Pseudallophtes falconis</i>	nasal cavity	Gaud 1983a
	<i>Ptilonyssus cerchneis</i>	nasal cavity	Fain 1957
	<i>Tytodectes cerchneis</i>	subcutaneous	Fain 1966b
	<i>Tytodectes falconis</i>	subcutaneous	Fain 1969
Red-footed Falcon (<i>Falco vespertinus</i>)	<i>Hieracolichus nisi</i>	feathers	Shumilo et al. 1973, Gaud 1983a

Appendix 1. Continued.

RAPTOR	MITE	HABITAT	REFERENCES
Barred Kestrel (<i>Falco zoniventris</i>)	<i>Aetacarus</i> sp.	feathers	Gaud 1983a
Barred Forest-Falcon (<i>Microastur ruficollis</i>)	Ingrassiinae sp. ^a	feathers	Philips and Fain 1991
Collared Falconet (<i>Microhierax caerulescens</i>)	<i>Coraciacarus</i> sp. ^b	feathers	McClure and Ratanaworabhan 1971
Philippine Falconet (<i>Microhierax erythrogenys</i>)	mites ^a	skin	Maa 1969
Yellow-headed Caracara (<i>Milvago chimachima</i>)	mites ^a	skin	Bequaert 1953
	<i>Ptilonyssus souzai</i>	nasal cavity	Pereira and Castro 1949
Crested Caracara (<i>Polyborus plancus</i>)	<i>Eutrombicula batatas</i>	skin/nest	Brennan and Yunker 1966
	<i>Hieracolicus</i> sp.	feathers	Kurey 1976
Family Sagittariidae			
Secretary-bird (<i>Sagittarius serpentarius</i>)	<i>Aetacarus laurencei</i>	feathers	Gaud 1983b

^a These mites were found on louseflies (Hippoboscidae) on the bird.
^b These are incorrectly identified or accidental records.
^c Nest record.
^d *Cheyletiella* is now restricted to mammal parasites; there are four other genera of bird parasites in the Family Cheyletiellidae.

Appendix 2. A list of the parasitic mites of the Strigiformes.

OWL	MITE	HABITAT	REFERENCES
Strigiformes	<i>Dermanyssus gallinae</i>	skin/nest	Pfister 1991
	Rhinonyssidae	nasal cavity	Butenko et al. 1972
Family Strigidae	<i>Glaucalges attenuatus</i>	feathers	Radford 1953, 1958
	<i>Kramerella lunulata</i>	feathers	Radford 1953, 1958
	<i>Kramerella lyra</i>	feathers	Radford 1953, 1958
	<i>Kramerella major</i>	feathers	Radford 1953, 1958
Northern Saw-whet Owl (<i>Aegolius acadicus</i>)	<i>Dermanyssus americanus</i>	skin/nest	Philips 1990
	<i>Petitota</i> sp.	feathers	Philips, present work
Boreal Owl (<i>Aegolius funereus</i>)	<i>Glaucalges attenuatus</i>	feathers	Niethammer 1938
	<i>Harpyrhynchus</i> n. sp.	skin	Philips 1993
	<i>Kramerella lunulata</i> ^a	feathers	Niethammer 1938, Dubinin 1953, Radford 1958
	<i>Kramerella major</i> ^{a,b}	feathers	Mégnin and Trouessart 1884a, Nordberg 1936, Dubinin 1953, Radford 1958
	<i>Kramerella mrciaki</i>	feathers	Cerný 1973, Mironov 1997
	<i>Kramerella</i> n. sp.	feathers	Philips, present work
	<i>Mesalgoides picimajoris</i> ^a	feathers	Lönnfors 1937
	<i>Paralges</i> sp. ^a	quills	Philips 1993
	<i>Passeroptes</i> n. sp.	skin	Philips 1990
	<i>Petitota aluconis</i>	feathers	Lönnfors 1937
	<i>Petitota haengii</i>	feathers	Mironov 1997
	<i>Rhinoecius aegolii</i>	nasal cavity	Butenko 1971, Philips 1993

Appendix 2. Continued.

OWL	MITE	HABITAT	REFERENCES
Marsh Owl (<i>Asio capensis</i>)	<i>Dermonoton parallelus</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1980
	<i>Kramerella oti</i>	feathers	Gaud 1980
	<i>Pandalura strigisoti</i>	feathers	Gaud 1980
	<i>Rhinoecius africanus</i>	nasal cavity	Zumpt and Patterson 1951, Zumpt and Till 1961
Short-eared Owl (<i>Asio flammeus</i>)	mites ^c	skin	Maa 1966
	<i>Dermonoton</i> sp.	feathers	Dubinin 1956
	<i>Glaucalges attenuatus</i>	feathers	Buchholz 1869
	<i>Kramerella flammei</i>	feathers	Lönnfors 1937
	<i>Kramerella lyra</i>	feathers	Mégnin and Trouessart 1884a, Radford 1958
	<i>Kramerella major</i>	feathers	Mégnin and Trouessart 1884a, Radford 1958
	<i>Kramerella oti</i>	feathers	Vasyukova et al. 1996
	<i>Kramerella</i> sp.	feathers	Kurey 1976
	<i>Leptotrombidium akamushi</i>	skin/nest	Wharton and Fuller 1952
	<i>Microlichus tridicola</i> ^f	skin	Fain et al. 1987
	<i>Pandalura strigisoti</i>	feathers	Rothschild and Clay 1952
	<i>Petitota aluconis</i>	feathers	Gaud 1980
	<i>Proctophyllodes polyxenus</i> ^a	feathers	Atyeo and Braasch 1966
	<i>Rhinoecius alifanovi</i>	nasal cavity	Butenko 1976
	chiggers (Trombiculidae)	skin/nest	Maa and Kuo 1965
	mites ^c	skin	Walter 1989
	<i>Dermanyssus americanus</i>	skin/nest	Moss 1978
	<i>Dermanyssus hirundinis</i>	skin/nest	Kutzer et al. 1982
	<i>Dermonoton parallelus</i>	feathers	Gaud 1980
Long-eared Owl (<i>Asio otus</i>)	<i>Eulaelaps stabularis</i> ^a	mammals	Kutzer et al. 1982
	<i>Glaucalges attenuatus</i>	feathers	Buchholz 1869, Canestrini and Kramer 1899, Radford 1953, 1958
	<i>Glycyphagus domesticus</i> ^{a,c}	nest	Büttiker and Cerný 1974
	<i>Harpyrhynchus asio</i>	skin	Fain 1972
	<i>Kramerella lyra</i>	feathers	Mégnin and Trouessart 1884a, Radford 1958
	<i>Kramerella oti</i>	feathers	Lönnfors 1937, Radford 1958, Vasiliev 1959, Cerný 1977, Gaud 1980
	<i>Kramerella</i> sp.	feathers	Kurey 1976
	<i>Microlichus avus</i> ^c	skin	Ash and Hughes 1952
	<i>Microlichus charadriicola</i> ^f	skin	Büttiker and Cerný 1974
	<i>Myialges macdonaldi</i> ^f	skin	Hill et al. 1967
	<i>Myialges nudus</i>	skin	Fain 1965, Fain and Grootaert 1996
	<i>Neotrombicula lipovskyi</i>	skin/nest	Loomis 1956
	<i>Pandalura strigisoti</i>	feathers	Buchholz 1869, Canestrini and Kramer 1899, Radford 1953, 1958, Kurey 1976, Cerný 1977
	<i>Myialges uncus</i> ^c	skin	Ash and Hughes 1952, Fain 1965
	<i>Rhinoecius brikinboricus</i>	nasal cavity	Butenko 1976
	<i>Rhinoecius oti</i>	nasal cavity	Cooreman 1946
	<i>Strelkoviacarus critesi</i> ^c	skin	Hill et al. 1967
	<i>Sternostoma strigitis</i>	nasal cavity	Butenko 1976

Appendix 2. Continued.

OWL	MITE	HABITAT	REFERENCES
Little Owl (<i>Athene noctua</i>)	<i>Neotrombicula autumnalis</i>	skin/nest	Koptzev et al. 1961
	<i>Glaucalges attenuatus</i>	feathers	Gaud 1958, 1980
	<i>Kramerella lunulata</i>	feathers	Haller 1878, Niethammer 1938, Dubinin 1953, Radford 1958, Gaud 1980
<i>Bubo</i> sp.	<i>Ornithogastia ariadnae</i>	skin/nest	Hushcha 1982
	<i>Pandalura strigisoti</i>	feathers	Gaud 1958, 1980
	<i>Rhinoecius subbisetosus</i>	nasal cavity	Bregetova 1965
	<i>Dermanyssus gallinae</i>	skin/nest	Strandtmann and Wharton 1958
	<i>Dermonoton bubonis</i> ^d	feathers	Gaud 1980
Spotted Eagle-Owl (<i>Bubo africanus</i>)	<i>Astrida caprimulgi</i>	nasal cavity	Fain 1956a, Zumpt and Till 1961
	<i>Dermonoton parallelus</i>	feathers	Gaud 1980
	<i>Glaucalges attenuatus</i>	feathers	Gaud 1980
	<i>Kramerella maculata</i>	feathers	Gaud 1980
	<i>Pandalura strigisoti</i>	feathers	Gaud 1980
	<i>Rhinoecius buboensis</i>	nasal cavity	Fain 1958, 1959b, 1960, Zumpt and Till 1961, Domrow 1969
Eurasian Eagle-Owl (<i>Bubo bubo</i>)	mites ^c	skin	Walter 1989
	<i>Dermonoton longiventer</i>	feathers	Sohn and Noh 1994
	<i>Glaucalges attenuatus</i>	feathers	Lönnfors 1937, Mumcuoglu and Müller 1974
	<i>Kramerella bubonis</i>	feathers	Lönnfors 1937, Dubinin 1953, Radford 1958, Mrciak and Brander 1967
	<i>Kramerella major</i>	feathers	Mégnin and Trouessart 1884a, Dubinin 1953, Radford 1958
	<i>Pandalura strigisoti</i>	feathers	Lönnfors 1937, Mumcuoglu and Müller 1974
	<i>Petitota bubonis</i>	feathers	Atyeo and Philips 1984, Sohn and Noh 1994
Verreaux's Eagle-Owl (<i>Bubo lacteus</i>)	<i>Dermonoton apoplax</i>	feathers	Gaud 1980
	<i>Dermonoton parallelus</i>	feathers	Gaud 1980
	<i>Glaucalges attenuatus</i>	feathers	Gaud 1980
	<i>Kramerella lobata</i>	feathers	Gaud 1980
	<i>Kramerella lunulata</i> ^a	feathers	Radford 1958
	<i>Pandalura strigisoti</i>	feathers	Gaud 1980
Akun Eagle-Owl (<i>Bubo leucostictus</i>)	<i>Dermonoton apoplax</i>	feathers	Gaud 1980
	<i>Glaucalges attenuatus</i>	feathers	Gaud 1980
	<i>Pandalura strigisoti</i>	feathers	Gaud 1980
Fraser's Eagle-Owl (<i>Bubo poensis</i>)	<i>Dermonoton apoplax</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1980
	<i>Glaucalges attenuatus</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1980
	<i>Pandalura strigisoti</i>	feathers	Gaud 1980
Shelley's Eagle-Owl (<i>Bubo shelleyi</i>)	<i>Glaucalges attenuatus</i>	feathers	Gaud 1980
	<i>Kramerella lobata</i>	feathers	Gaud 1980
	<i>Pandalura strigisoti</i>	feathers	Gaud 1980

Appendix 2. Continued.

OWL	MITE	HABITAT	REFERENCES
Great Horned Owl (<i>Bubo virginianus</i>)	mites ^c	skin	Bequaert 1953, Maa 1969
	<i>Blattisocius keegan</i> ^{a,c}	trees	Philips and Fain 1991
	<i>Bubophilus ascalaphus</i>	quills	Philips and Norton 1978
	<i>Dermonoton</i> sp. ^d	feathers	Kurey 1976
	Epidermoptidae ^c	skin	Herman 1945
	<i>Euschoengastia numerosa</i>	skin/nest	Wrenn and Loomis 1974
	<i>Glaucalgas attenuatus</i>	feathers	Atyeo and Philips 1984
	<i>Harpyrhynchus</i> sp.	skin	Philips, present work
	<i>Knemidocoptes mutans</i>	skin	Schulz et al. 1989, Schulz 1990, Malley and Whitbread 1996, Houston et al. 1998
	<i>Kramerella</i> n. sp.	feathers	Philips and Norton 1978, Atyeo and Philips 1984, Philips 1993
	<i>Myialges anchora</i> ^f	skin	Furman and Tarshis 1953, Bequaert 1953, Fain 1965
	<i>Pandalura strigisoti</i>	feathers	Atyeo and Philips 1984
	<i>Paralges</i> n. sp.	quills	Philips 1993
	<i>Petitota bubonis</i>	feathers	Atyeo and Philips 1984
	<i>Pneumophagus bubonis</i>	lungs	Fain and Smiley 1989
	<i>Proctophyllodes polyxenus</i> ^a	feathers	Atyeo and Braasch 1966
	<i>Rhinoecius grandis</i>	nasal cavity	Strandtmann 1952
	<i>Neotytodectes mexicanus</i> ^b	subcutaneous	O'Connor 1981
	<i>Glaucidium</i> sp.	skin/nest	Brennan and Jones 1960, Loomis 1969
Ferruginous Pygmy-Owl (<i>Glaucidium brasilianum</i>)	<i>Eutrombicula alfreddugesi</i>	skin/nest	Brennan and Jones 1960, Loomis 1969
Asian Barred Owlet (<i>Glaucidium cuculoides</i>)	<i>Rhinoecius bisetosus</i>	nasal cavity	Strandtmann 1960, Wilson 1968
Mountain Pygmy-Owl (<i>Glaucidium gnoma</i>)	<i>Kramerella</i> sp.	feathers	Kurey 1976
Eurasian Pygmy-Owl (<i>Glaucidium passerinum</i>)	<i>Dermonoton eventratus</i>	feathers	Canestrini and Kramer 1899, Dubinin 1956, Radford 1953, 1958
	<i>Kramerella glaucidii</i>	feathers	Mrciak and Brander 1967, Cerný and Wiesner 1992
Pearl-spotted Owlet (<i>Glaucidium perlatum</i>)	<i>Astrida caprimulgi</i>	nasal cavity	Fain 1956a, Zumpt and Till 1961
Cuban Pygmy-Owl (<i>Glaucidium siju</i>)	<i>Tytodectes glaucidii</i>	subcutaneous	Fain 1967, Cerný 1969
Barking Owl (<i>Ninox connivens</i>)	<i>Leptotrombidium nissani</i>	skin/nest	Domrow 1974, Domrow and Lester 1985
	<i>Neoschoengastia americana</i>	skin/nest	Domrow and Lester 1985
	<i>Rhinoecius cooremani</i>	nasal cavity	Domrow 1969, 1987
	<i>Odontacarus trisetosus</i>	skin/nest	Goff 1979
Solomon Hawk-Owl (<i>Ninox jacquinoti</i>)			
Morepork (<i>Ninox novaeseelandiae</i>)	<i>Leptotrombidium nissani</i>	skin/nest	Domrow 1974, Domrow and Lester 1985
	<i>Neoschoengastia americana</i>	skin/nest	Domrow and Lester 1985
	<i>Rhinoecius cooremani</i>	nasal cavity	Domrow 1967, 1987
New Britain Hawk-Owl (<i>Ninox odiosa</i>)	mites ^c	skin	Maa 1966
Philippine Hawk-Owl (<i>Ninox philippensis</i>)	Analgidae ^c	skin	Philips and Fain 1991
	<i>Oconnoria inexpectata</i>	quills	Gaud et al. 1989
Snowy Owl (<i>Nyctea scandiaca</i>)	<i>Knemidocoptes</i> sp.	skin	Cooper 1978, 1985
	<i>Rhinoecius nyctae</i>	nasal cavity	Butenko 1976

Appendix 2. Continued.

OWL	MITE	HABITAT	REFERENCES
<i>Otus</i> sp.	<i>Myialges bombycillae</i> ^c	skin	Philips and Fain 1991
Eastern Screech-Owl (<i>Otus asio</i>)	mites ^c	skin	Bequaert 1953, Fain 1965, Maa 1969
	<i>Dermanyssus americanus</i>	skin/nest	Ewing 1925, 1936, Radford 1950, Evans and Till 1962, Moss 1978
	<i>Dermonoton</i> sp.	feathers	Kurey 1976
	<i>Harpyrhynchus</i> sp.	skin	Philips 1993
	<i>Miyatrombicula cynos</i> ^b	skin/nest	Philips 1978, Philips and Dindal 1990
Variable Screech-Owl (<i>Otus atricapillus</i>)	<i>Neoschoengastia americana</i>	skin/nest	Everett et al. 1972
	Syringophilidae	quills	Johnston and Kethley 1973
	<i>Blankaartia sinnamaryi</i>	skin/nest	Brennan and Yunker 1966
Indian Scops-Owl (<i>Otus bakamoena</i>)	chiggers (Trombiculidae)	skin/nest	Maa and Kuo 1965
	feather mites	feathers	Maa and Kuo 1965
	<i>Dermonoton</i> sp.	feathers	McClure and Ratanaworabhan 1971
	<i>Leptotrombidium deliense</i>	nest/skin	McClure and Ratanaworabhan 1971
	<i>Ornithonyssus bursa</i>	skin/nest	McClure and Ratanaworabhan 1971
	<i>Rhinoecius cavannus</i>	nasal cavity	Wilson 1968, McClure and Ratanaworabhan 1971
	<i>Toritrombicula densipiliata</i>	skin/nest	Nadchatram 1967, Vercammen-Grandjean and Langston 1976
	<i>Toritrombicula vorca</i>	skin/nest	Vercammen-Grandjean and Langston 1976
White-faced Scops-Owl (<i>Otus leucotis</i>)	<i>Pandalura strigisoti</i>	feathers	Gaud 1980
Reddish Scops-Owl (<i>Otus rufescens</i>)	<i>Leptotrombidium deliense</i>	skin/nest	McClure and Ratanaworabhan 1971
Eurasian Scops-Owl (<i>Otus scops</i>)	<i>Toritrombicula densipiliata</i>	skin/nest	McClure and Ratanaworabhan 1971
	chiggers (Trombiculidae)	skin/nest	Maa and Kuo 1965
	feather mites	feathers	Maa and Kuo 1965
	mites ^c	skin	Maa 1969
	<i>Dermonoton parallelilobus</i> ^a	feathers	Radford 1953, 1958
	<i>Dermonoton parallelus</i>	feathers	Mégnin and Trouessart 1884c, Canestrini and Kramer 1899, Dubinin 1956, Gaud and Till 1961
	<i>Dermonoton</i> sp.	feathers	McClure and Ratanaworabhan 1971
	<i>Kramerella lunulata</i>	feathers	Dubinin 1953
	<i>Kramerella lyra</i>	feathers	Dubinin 1953
	<i>Kramerella major</i>	feathers	Shumilo et al. 1973
	<i>Leptotrombidium deliense</i>	skin/nest	McClure and Ratanaworabhan 1971
African Scops-Owl (<i>Otus senegalensis</i>)	<i>Neoschoengastia longipes</i>	skin/nest	McClure and Ratanaworabhan 1971
	<i>Astrida caprimulgi</i>	nasal cavity	Fain 1956a, Zumpt and Till 1961
Mountain Scops-Owl (<i>Otus spilocephalus</i>)	<i>Astrida caprimulgi</i>	nasal cavity	Fain 1963a
	<i>Dermonoton</i> sp.	feathers	McClure and Ratanaworabhan 1971
	<i>Leptotrombidium scutellare</i>	skin/nest	McClure and Ratanaworabhan 1971
	<i>Neoschoengastia</i> sp.	skin/nest	McClure and Ratanaworabhan 1971
Whiskered Screech-Owl (<i>Otus trichopsis</i>)	<i>Dermonoton</i> sp.	feathers	Kurey 1976
Band-bellied Owl (<i>Pulsatrix melanota</i>)	<i>Rhinoecius nyctae</i>	nasal cavity	Amaral 1962
Vermiculated Fishing-Owl (<i>Scotopelia bouvieri</i>)	<i>Dermonoton parallelilobus</i>	feathers	Gaud 1980

Appendix 2. Continued.

OWL	MITE	HABITAT	REFERENCES
Pel's Fishing-Owl (<i>Scotopelia peli</i>)	<i>Dermonoton parallelilobus</i>	feathers	Gaud and Mouchet 1959b, Gaud and Till 1961, Gaud 1980
	<i>Glaucalges attenuatus</i>	feathers	Gaud and Till 1961, Gaud 1980
	<i>Pandalura strigisoti</i>	feathers	Gaud 1980
Burrowing Owl (<i>Speotyto cunicularia</i>)	<i>Dermonoton</i> sp.	feathers	Kurey 1976
	<i>Euschoengastoides gurneyi</i>	skin/nest	Loomis 1956
	<i>Hypodectes propus</i> ^a	subcutaneous	Pence and Bergan 1996
	<i>Hyponeocula montanensis</i>	skin/nest	Loomis 1956
	<i>Kramerella major</i>	feathers	Mégnin and Trouessart 1884a, Dubinin 1953, Radford 1958
	<i>Neoschoengastia americana</i>	skin/nest	Loomis 1956, Everett et al. 1972
	<i>Proctophyllodes polyxenus</i> ^a	feathers	Atyeo and Braasch 1966
	<i>Rhinoecius bisetosus</i>	nasal cavity	Strandtmann 1952, Amaral 1962
	<i>Sternostoma augei</i>	nasal cavity	Amaral 1962
	<i>Tytodectes speotyto</i>	subcutaneous	Pence and Bergan 1996
Tawny Owl (<i>Strix aluco</i>)	<i>Dermanyssus hirundinis</i> ^b	skin/nest	Zeman and Jurik 1981
	<i>Glaucalges attenuatus</i>	feathers	Atyeo pers. comm.
	<i>Kramerella aluconis</i>	feathers	Lönnfors 1937, Dubinin 1953, Radford 1958, Shumilo et al. 1973
	<i>Kramerella major</i>	feathers	Dubinin 1953, Radford 1958
	<i>Pandalura strigisoti</i>	feathers	Gaud 1958, 1980
	<i>Petitota aluconis</i>	feathers	Buchholz 1869, Radford 1953, 1958
		feathers	Maa and Kuo 1965
		feathers	
Brown Wood-Owl (<i>Strix leptogrammica</i>)	feather mites	feathers	
Great Grey Owl (<i>Strix nebulosa</i>)	<i>Dermonoton parallelilobus</i>	feathers	Mégnin and Trouessart 1884c, Canestrini and Kramer 1899, Radford 1953, 1958, Dubinin 1956, Gaud and Till 1961, Gaud 1980
	<i>Kramerella aprotuberantia</i>	feathers	Philips, present work
	<i>Pandalura strigisoti</i>	feathers	Philips, present work
	<i>Passeroptes</i> n. sp.	skin	Philips, present work
	<i>Petitota</i> sp.	feathers	Philips, present work
Spotted Owl (<i>Strix occidentalis</i>)	<i>Euschoengastia</i> sp. (probably <i>numerosa</i>)	skin/nest	Hunter et al. 1994, Gutiérrez et al. 1995
Mottled Wood-Owl (<i>Strix ocellata</i>)	<i>Myialges bombycillae</i>	skin	Philips and Fain 1991
Ural Owl (<i>Strix uralensis</i>)	<i>Kramerella aprotuberantia</i>	feathers	Dubinin 1953, Radford 1958
	<i>Petitota aluconis</i>	feathers	Niethammer 1938
Barred Owl (<i>Strix varia</i>)	<i>Dermonoton</i> sp.	feathers	Kurey 1976
	<i>Dermonoton parallelilobus</i>	feathers	Banks 1915
	<i>Kramerella</i> sp.	feathers	Kurey 1976
	<i>Ornithonyssus</i> sp.	feathers	Peters 1936
	<i>Pandalura strigisoti</i>	feathers	Atyeo pers. comm.
	<i>Paralges</i> n. sp.	quills	Philips, present work
	<i>Passeroptes</i> n. sp.	skin	Philips, present work
	<i>Rhinoecius cooremani</i>	nasal cavity	Strandtmann 1952, Pence 1973
	<i>Blankaartia sinnamaryi</i>	skin/nest	Brennan and Yunker 1966
Mottled Owl (<i>Strix virgata</i>)	<i>Eutrombicula alfreddugesi</i>	skin/nest	Brennan and Jones 1960, Loomis 1969
African Wood-Owl (<i>Strix woodfordii</i>)	<i>Dermonoton</i> spp.	feathers	Cheke 1972, 1978
	<i>Glaucalges attenuatus</i>	feathers	Gaud 1980
Northern Hawk Owl (<i>Surnia ulula</i>)	<i>Kramerella major</i>	feathers	Mégnin and Trouessart 1884a, Dubinin 1953, Radford 1958

Appendix 2. Continued.

OWL	MITE	HABITAT	REFERENCES
	<i>Kramerella</i> sp.	feathers	Vasyukova et al. 1996
Family Tytonidae			
Congo Bay-Owl (<i>Phodilus prigoginei</i>)	<i>Dermonoton parallelus</i>	feathers	Gaud 1980
Barn Owl (<i>Tyto alba</i>)	mites ^c	skin	Maa 1969
	<i>Aureliania aureliani</i>	nasal cavity	Fain 1956b, 1963b, Zumpt and Till 1961, Domrow 1969, 1991
	<i>Dermonoton sclerourus</i>	feathers	Gaud 1980, D'Souza et al. 1986
	<i>Dermonoton</i> sp.	feathers	McClure and Ratanaworabhan 1971
	<i>Glaucalges attenuatus</i>	feathers	Rothschild and Clay 1952, Radford 1958, Gaud 1958, 1980, Gaud and Till 1961, Cerný 1967, D'Souza et al. 1986
	<i>Glaucalges</i> sp.	feathers	McClure and Ratanaworabhan 1971, Kurey 1976
	<i>Harpyrhynchus tyto</i>	skin	Fain 1972
	<i>Kramerella lunulata</i>	feathers	Niethammer 1938, Gaud and Petitot 1948a, Cerný 1967, Bunn et al. 1982
	<i>Kramerella lyra</i>	feathers	Radford 1958
	<i>Kramerella quadrata</i>	feathers	Gaud 1980
	<i>Kramerella</i> sp.	feathers	Kurey 1976
	<i>Leptotrombidium nissani</i>	skin/nest	Domrow 1974, Domrow and Lester 1985
	<i>Neoboydaia</i> sp.	nasal cavity	Dusbábek and Cerný 1970
	<i>Neottialges evansi</i> ^a	subcutaneous	Pence and Bergan 1996
	<i>Ornithonyssus bursa</i>	skin/nest	Domrow 1977
	<i>Ornithonyssus sylviarum</i>	skin/nest	Cooper 1978
	<i>Ornithonyssus</i> sp.	skin/nest	Keymer 1972
	<i>Pandalura strigisoti</i>	feathers	Niethammer 1938, Radford 1958, Gaud 1958, Gaud and Mouchet 1959a, Gaud and Till 1961, Gaud 1980
	<i>Rhinoecius tytonis</i>	nasal cavity	Fain 1956c, 1959a, Zumpt and Till 1961, Domrow 1969
	<i>Tytodectes strigis</i>	subcutaneous	Gene 1848, Fain 1967, Wurst and Havelka 1997
	<i>Tytodectes tyto</i>	subcutaneous	Fain 1966b, 1967, Pence and Bergan 1996
African Grass-Owl (<i>Tyto capensis</i>)	<i>Dermonoton sclerourus</i>	feathers	Gaud 1980
	<i>Kramerella quadrata</i>	feathers	Gaud 1980
Australian Masked-Owl (<i>Tyto novaehollandiae</i>)	mites ^c	skin	Maa 1966
	<i>Tytodectes tyto</i>	subcutaneous	Domrow 1992

^a These are incorrectly identified or accidental records.
^b Nest record.
^c These mites were found on louseflies (Hippoboscidae) on the bird.
^d *Dermonoton bubonis* from *Bubo* sp. (Gaud 1980) is actually an invalid nomen nudum for an undescribed species of *Dermonoton* from *Bubo virginianus* (Gaud pers. comm.).

SHORT COMMUNICATIONS

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DIURNAL VOCAL ACTIVITY OF YOUNG EAGLE OWLS AND ITS IMPLICATIONS IN DETECTING OCCUPIED NESTS

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KEY WORDS: *Eagle Owl*, *Bubo bubo*; *diurnal calling activity*; *food- and contact-call*; *call practice*; *occupied nest census*; *productivity evaluation*.

Vocal surveys are used extensively to locate nests and estimate numbers of birds (Ralph and Scott 1981, Fuller and Mosher 1987, Ralph et al. 1995, Stewart et al. 1996). They are particularly useful for nocturnal birds that cannot be easily located during the day (Reid et al. 1999). Due to the crepuscular and nocturnal habits of owls, numerous census techniques have been developed (Fuller and Mosher 1981, Smith 1987). They include visual searches, passive auditory surveys (Reid et al. 1999), location of roosts and nests, and use of tape-recorded calls to elicit responses (acoustic-lure survey, Reid et al. 1999).

When a species is being censused, it is essential to have a good knowledge of its behavior and breeding cycle to ensure accuracy of the results (e.g., broadcasting of tape-recorded vocalizations when the probability that birds are near the nest is high). For this reason, it is essential to study the behavior of species to be censused. Myserud and Dunker (1982) and Penteriani and Pinchera (1991) concluded that passive auditory surveys of adult Eagle Owls (*Bubo bubo*) were most reliable for locating nests because the owls did not consistently respond to playback of their vocalizations, especially when they had nestlings or fledglings. Although playback and passive auditory surveys of adult Eagle Owls have been used extensively to locate territories (e.g., Bergerhausen and Willems 1988, Penteriani 1996), no one has investigated the possibility that passive auditory surveys of juveniles might also be useful for surveying Eagle Owls. Data on the vocal activity pattern and distribution of young Eagle Owls are scarce, although their call rates are very high (Kranz 1971, Mikkola 1983).

To investigate the possibility of using passive auditory surveys of juvenile Eagle Owls to locate nests and fledged young during the day, we studied diurnal patterns of vocalizations of nestling and fledgling Eagle Owls in southern France. The study was prompted by field observations that indicated that young Eagle Owls were particularly vociferous during the day (V. Penteriani and M. Gallardo unpubl. data).

METHODS

The study was conducted during 1999 on Luberon Mountain in southern France (43°53'N, 5°24'E). Elevation ranged from 160 m in the Durance River valley to 1125 m on Grand Luberon ridge. The study area was characterized by a mosaic of rock cliffs, shrub vegetation (*Quercus coccifera*, *Thymus vulgaris*, and *Rosmarinus officinalis*), Mediterranean forest (*Quercus ilex*, *Q. pubescens*, and *Pinus halepensis*), croplands, pastures, and fallow fields.

We systematically listened to young Eagle Owls from the age of about 3 wk (nestlings), when their calls are easily distinguishable, to about 8 wk (fledglings), when their calls begin to resemble those of adults (Glutz Von Blotzheim and Bauer 1980) and their diurnal vocal activity near the nest seems to decrease (V. Penteriani unpubl. data). During this period (May to July in our study area), we recorded both frequency and distribution of the main call type of young owls, the dry rasping *chwätch*, considered as a food-call (Cramp and Simmons 1980). For passive auditory surveys, we divided each day into 14 1-hr intervals, from sunrise to sunset, and evenly distributed surveys (on a rotation basis) among nine owlets (two young in a nest in four cases, one young alone in one case), randomly selected inside the study area. We distributed the surveys over the May–July period to obtain data on the vocal activity of each individual for the entire length of each solar day at the end of the eighth week of life. In each observation period, we collected the time of start of a vocal event, duration of the vocal event, and

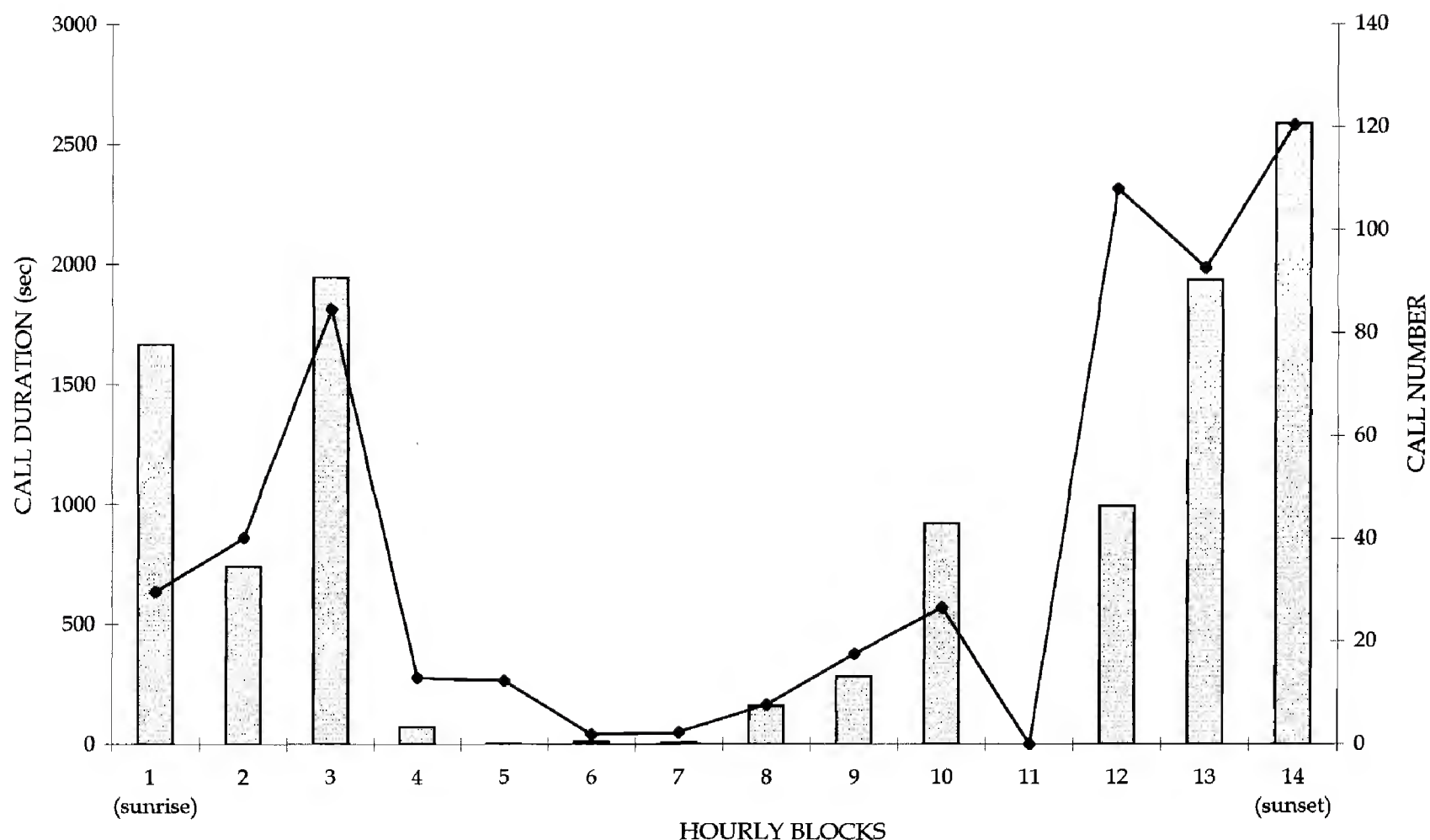


Figure 1. Diurnal vocal activity of nine young Eagle Owls in southern France: mean duration of vocalizations (sec; grey bars) and mean number of calls (solid line) by time of day. Hourly blocks represent the intervals of the day, from sunrise to sunset.

the number of vocal events. We used a stopwatch to determine the duration of a given vocal event and we identified the end of a vocal event as the last call heard more than 60 sec before the next call (i.e., 1 min of silence between calls or between sequences was regarded as a dividing unit of time). Isolated calls were arbitrarily assigned a duration of 1 sec. We did not conduct observations on windy or rainy days and always recorded vocalizations from the same location and from the same distance (<500 m from the nesting cliff). We always remained out of sight of the owls because the presence of humans alters the behavior of the young.

We used a Repeated Measures ANOVA (Sokal and Rohlf 1995) to compare the duration of vocalizations and the number of calls throughout the day. We used the Spearman rank correlation coefficient to determine a possible common pattern between the duration of the vocal events and the call number characterizing them (Sokal and Rohlf 1995).

RESULTS

The duration of vocalizations (Fig. 1; $F_{8,13} = 47.36$, $P < 0.001$) and the number of calls (Fig. 1; $F_{8,13} = 38.73$, $P < 0.001$) were significantly different in the various hourly blocks, with peaks occurring during 3 hrs after sunrise and 3 hrs before sunset (Fig. 1). A common positive pattern between the duration of the vocal events and the number of calls was observed ($r_s = 0.85$, $P < 0.001$,

Spearman rank). The mean number of calls per series was 65.6 ± 127.1 (\pm SD, range = 1–259) (Fig. 1). Duration of vocalizations in a single series ranged from 1–1130 sec ($\bar{x} = 808.4 \pm 891.4$ sec). The maximum time interval between two neighboring series was 40 min, during the hourly block corresponding to 5 hr after sunrise. The mean interval between calls was 10.5 ± 6.02 sec (range = 2–28.7). During the passive auditory periods, all nine juveniles were heard, always in the immediate vicinity of the nest hole, even after they left the nest. In four cases where we observed adults near juveniles that were calling, the adults appeared to ignore the juveniles.

DISCUSSION

Our findings that vocalizations peaked 3 hr before sunset and 3 hr after sunrise highlighted the diurnal activity of this dominantly crepuscular and nocturnal species. The typical *chwätsch* call of nestling and fledgling Eagle Owls has been described as a food call (Cramp and Simmons 1980), but its high diurnal frequency, use during the period of the day coinciding with low adult activity (although young are regularly fed during the day by females, L. Dalbeck pers. comm.), and observed indifference of adults to this type of behavior make it difficult to explain how this call is used for feeding alone. It may, in fact, be a method of communicating within family

groups (e.g., contact call). Fledglings of some suboscine species use their song as a contact call in their early stages of life (Kroodsma 1984) when they are just beginning to learn sounds in their environment and recognizable production of those sounds occurs a month or more later, and only after extensive practice, or subsong (Kroodsma 1981). The high rates of diurnal vocalizations in Eagle Owls may simply result from young owls practicing their voices, just as high rates of diurnal activity may represent muscular exercise (e.g., flight training).

Our results suggest that passive auditory surveys of young Eagle Owls are effective when owlets are 5–8-wk old, and are most effective during the 3-hr period after sunrise and preceding sunset. Listening sessions must be 40 min in duration. Although, in these hourly blocks, we always heard young Eagle Owl calls, we suggest two listening sessions as a precaution before considering a site as not occupied by a successfully breeding pair. Since we did not conduct surveys in the hours before sunrise and after sunset, we cannot address survey effectiveness during those periods. We recommend that listening points be selected such that they are hidden from the owls' view and at a maximum distance of 500 m from potential nesting sites, especially in noisy areas. Although the calls of young can be heard on silent nights as far as 500 m away, the background noise during diurnal hours makes listening sessions problematic. Days with wind (>15 km/hr) and intense precipitation are unsuitable for conducting surveys with this technique.

Our results suggest that passive auditory surveys during the day are useful for surveying Eagle Owls because young are normally very vocal during the day, surveys can be conducted at a time of day and year when adults are relatively secretive, and they allow estimation of the minimum number of young produced.

It would be interesting to determine if diurnal calls are typical of Eagle Owls in other European countries and of congeners. For example, it seems that there are obvious differences in diurnal call behavior between our study area and western Germany, where the calls of young are irregular during the day (W. Bergerhausen and L. Dalbeck pers. comm.). The Great Horned Owl (*Bubo virginianus*) is the geographical and ecological counterpart of the Eurasian Eagle Owl. The reasons for treating this as a distinct species have rarely been made clear (Voous 1988). It would be interesting to investigate whether the vocal behavior of young Great Horned Owls has patterns similar to those of the Eagle Owl. The Great Horned Owl seems to be relatively silent during the day, probably because diurnal begging juveniles could be subject to higher rates of predation by Northern Goshawks (*Accipiter gentilis*) and Red-tailed Hawks (*Buteo jamaicensis*), or "mobbing" by jays and crows (E. Forsman unpubl. data). However, passive surveys are useful for locating young Great Horned Owls at night or just before sunrise or after sunset, when they are quite vocal (E. Forsman unpubl. data).

RESUMEN.—Al censar aves, es esencial saber su comportamiento y ciclo reproductivo para asegurar la veracidad de los resultados. En el caso de *Bubo bubo*, un método efectivo de investigación es el de utilizar un método pasivo de audición de vocalizaciones espontáneas de adultos. Sin embargo, se conoce poco acerca de los patrones y distribución de la actividad vocal de juveniles, los cuales vociferan bastante durante el día. Observamos el comportamiento de vocalización de juveniles de búhos en el sur de Francia para determinar si pueden ser localizados consistentemente durante el día utilizando un método pasivo de audición. La duración de las vocalizaciones ($F_{8,13} = 47.36$, $P < 0.001$) y el número de vocalizaciones ($F_{8,13} = 38.73$, $P < 0.001$) fue significativamente diferente en distintos momentos del día, la duración de las vocalizaciones diurnas fueron mayores en las primeras 3 horas del amanecer y en las 3 horas antes del atardecer. Escuchar las vocalizaciones espontáneas de juveniles puede ser considerado como un método útil para el monitoreo de búhos debido a que estos vociferan bastante durante el día. Las investigaciones deben llevarse a cabo para estimar un número mínimo de juveniles producidos. Nuestros resultados indican que la alta actividad diurna de juveniles puede estar relacionada con la necesidad de comunicarse entre el grupo familiar (i.e., vocalizaciones de contacto) para estimular la alimentación por parte de los adultos o practicar sus vocalizaciones.

[Traducción de César Márquez]

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FOOD HABITS OF THE STRIPED OWL (*ASIO CLAMATOR*) IN BUENOS AIRES PROVINCE, ARGENTINA

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KEY WORDS: *Striped Owl*; *Asio clamator*; *food habits*; *Argentina*.

The Striped Owl (*Asio clamator*) is a widespread species from Mexico through tropical and subtropical South America to Argentina (Grossman and Hamlet 1964, Canevari et al. 1991, Holt et al. 1999). It inhabits deciduous seasonal forests, lowland seasonal forests, gallery forests, lowland savannas, desert forests, and grasslands (Grossman and Hamlet 1964, Canevari et al. 1991, Holt et al. 1999). Despite its widespread distribution, the status of the Striped Owl is poorly known (Burton 1973, Holt et al. 1999) and it is con-

sidered to be a rare species in Buenos Aires Province in Argentina (Narosky and Di Giacomo 1993).

Studies of the Striped Owl in Argentina have focused mainly on anecdotal aspects of its biology and breeding ecology (e.g., Bledinger et al. 1987, Martínez et al. 1996). Its diet is poorly studied but the limited information that is available indicates that it preys mainly on small mammals (Grossman and Hamlet 1964, Burton 1973, Phelps and Meyer de Schauensee 1994) followed by birds, reptiles, and insects (Holt et al. 1999). Here, we report on the diet of Striped Owls in the southernmost extreme of its distribution in the southeastern portion of Buenos Aires Province, Argentina.

METHODS

Our study was carried out in Mar Chiquito Biosphere Reserve (37°40'S, 57°23'W), Buenos Aires Province, Argentina. The reserve covers 30 000 ha and supports a diverse array of habitats including ponds, salt marshes,

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grasslands, woodlands, exotic tree plantations, and agricultural fields.

We found a pair of Striped Owls in an area of tala (*Celtis tala*) forest at Nahuel Rucá Ranch. The tala forest is derived from thorn forests (Espinal) and this relict patch represents the southernmost extreme of Espinal forest in Argentina. The patch covered a 6 ha area and was surrounded by a pond and grazed native grassland. There were a few houses and a plantation of eucalyptus (*Eucalyptus* spp.) trees nearby.

From August to November 1997, pellets and prey remains were collected in different plucking stations and roosting sites of the owls. Bird, mammal, and insect remains were identified based on bones, feathers, bills, hair, dentaries, and exoskeletons, and compared with the collections of Laboratorio de Vertebrados, Facultad de Ciencias Exactas y Naturales-Universidad Nacional de Mar del Plata and Museo Municipal de Ciencias Naturales “Lorenzo Scaglia” de Mar del Plata. The majority of prey were identified to species level. Bird and mammal weights were obtained from the literature (Salvador 1988, Camperi 1992, Redford and Eisenberg 1992) and unpublished data (M. Kittlein pers. comm.). A weight of 1 g was assigned to each insect prey species (Jiménez 1993).

RESULTS AND DISCUSSION

A total of 56 prey items was identified from 34 pellets and 3 prey remains (pile of feathers). Rodents were the main prey (55.4%) followed by birds (42.9%) and insects (1.8%, Table 1). *Rattus* spp. was the most common prey item (43%). Among birds, Rufous-collared Sparrows (*Zonotrichia capensis*, 23.2%) and Eared Doves (*Zenaida auriculata*, 17.9%) were most frequently taken. Other items comprised only a small fraction of the diet (16.2%).

Prey weights ranged from a low of 1 g in the case of insects to a high 630 g in the case of *Cavia aperea* (Table 1). Rodents comprised up to 81.5% of prey by weight and *Rattus* spp. contributed with the highest value (66.9%) followed by *Cavia aperea* (14%). The occurrence of adult *C. aperea* in the diet was surprising, since they weigh more than one and a half times as much as Striped Owls (maximal weight recorded of Striped Owl is 485 gr, Salvador 1988). We were not certain if *C. aperea* were eaten as carrion or actually hunted but Striped Owls are highly adapted to hunt live prey (Holt et al. 1999). The biomass contribution of birds was minor (20.1%) with Eared Doves contributing the largest amount (12%, Table 1). Other studies have confirmed that birds are common in the diets of Striped Owls (Grossman and Hamlet 1964, Burton 1973, Phelps and Meyer de Schauensee 1994, Holt et al. 1999).

Our results agree with those of Martínez et al. (1996) who studied the diet of Striped Owls in an area of shrub and exotic trees in Laguna de Los Padres Reserve, located 35 km north of Nahuel Ruca in Buenos Aires Province. They recorded seven bird and mammal species in the diet; three of which (*Reithrodon auritus*, *Holochilus brasiliensis*, and *Carduelis magellanica*) were absent in the diet of the Striped Owls we studied.

Table 1. Frequency of prey items, weight of individual prey and total percent biomass of prey in the diet of Striped Owl (*Asio clamator*) in Mar Chiquito Biosphera Reserve, Buenos Aires Province, Argentina.

PREY	FRE- QUENCY (%)	INDIVIDUAL WEIGHT (g)	TOTAL BIOMASS (%)
Aves			
Columbiformes			
Columbidae			
<i>Zenaida auriculata</i>	17.9	134.6	15.0
Passeriformes			
Emberizidae			
<i>Sicalis luteola</i>	1.8	16	1.8
<i>Zonotrichia capensis</i>	23.2	22.5	3.3
Mammalia			
Rodentia			
Caviidae			
<i>Cavia aperea</i> (adult)	3.6	630	7.0
<i>Cavia aperea</i> (young)	1.8	315	7.0
Muridae			
<i>Akodon azarae</i>	1.8	21	0.2
<i>Calomys musculus</i>	3.6	10	0.2
<i>Oryzomys flavescens</i>	1.8	17	0.2
<i>Rattus</i> spp.	43.0	250	66.9
Insecta			
Coleoptera			
Scarabaeidae			
<i>Sulcophanaeus menelas</i>	1.8	1	0.0

The Striped Owl is typically found in woodlands, forests, and savannas of tropical and subtropical zones (Grossman and Hamlet 1964). Our data show that it also occurs in the temperate-warm zone that corresponds to the Pampean Fitogeographic (Chaqueño Dominion, Cabrera 1976). In the past, this zone was dominated by tall grasslands without trees. Perhaps Striped Owls occur here because there is a natural corridor of tala forest which extends from the Entre Rios Province to Mar Chiquita Lagoon (Vervoorst 1967).

RESUMEN.—Se presenta información sobre la dieta del Lechuzón Orejudo (*Asio clamator*) en base al análisis de pellets (*N* = 34) y restos presa (*N* = 3), en el extremo Sur de su distribución Provincia de Buenos Aires, Argentina. Se identificaron 56 items presa, correspondiendo el 55.4% a los mamíferos, el 42.9% a las aves y el 1.8% a los insectos. El rango de pesos presa consumidos por esta lechuza fue de 1g a 630 g. El ítem mejor representado tanto en número (43%) como en biomasa (66.9%) fue *Rattus* spp. seguido en importancia numérica por el Chingolo Común (*Zonotrichia capensis*, 23.2%) y la Torcaza (*Zenaida auriculata*, 17.9%). A nivel de las aves el mayor aporte de biomasa fue dado por *Z. auriculata* (15%).

[Traducción de Autores]

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DIET OF BREEDING CINEREOUS HARRIERS (*CIRCUS CINEREUS*) IN SOUTHEASTERN BUENOS AIRES PROVINCE, ARGENTINA

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KEY WORDS: *Cinereous Harrier*, *Circus cinereus*; *breeding diet*, *trophic niche breadth*, *Argentina*.

The Cinereous Harrier (*Circus cinereus*), one of two South American harriers, is widespread and distributed from Colombia and Ecuador, through Perú, Bolivia and Paraguay, southwestern Brazil to Tierra del Fuego and Islas Malvinas (Grossman and Hamlet 1964, Canevari et al. 1991, del Hoyo et al. 1994). In Argentina, it is most

common in Patagonia and Islas Malvinas (Narosky and Yzurieta 1987) but it has also been recorded throughout northwestern, central and, occasionally, the northeastern parts of the country (Canevari et al. 1991). The Cinereous Harrier inhabits savannas, grasslands, wetlands, marshes, lagoons, shrubsteppes, and shrublands 0–4500 m elevation (Jiménez and Jaksic 1988, Canevari et al. 1991, Narosky and Di Giacomo 1993, del Hoyo et al. 1994).

Little has been reported about the Cinereous Harrier. The few previous studies of this species have focused on aspects of ecology and behavior (Jiménez and Jaksic

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1988) and breeding biology (Narosky and Yzurieta 1973, Saggese and De Lucca 1995). General information about its feeding habits suggests that it eats birds, small mammals, and reptiles (Humphrey et al. 1970, De La Peña 1985, Canevari et al. 1991, del Hoyo et al. 1994). Its diet has only been analyzed in detail in southernmost Chile (Jiménez and Jaksic 1988), where it preys on insects, birds, mammals, reptiles, and arachnids. In this paper, we report on the breeding season diet and trophic niche breadth of the Cinereous Harrier in the Pampas Zone of Argentina.

METHODS

The study was carried out in Laguna de los Padres Integral Reserve (37°56'S, 57°44'W), located 16 km west of Mar del Plata City, in southeastern Buenos Aires Province. The reserve is 680 ha in size, with a gentle relief composed of low hills and plains. The climate is subhumid to humid with a mean annual temperature of 13.8°C and a mean annual precipitation of about 844 mm (J. Cionchi unpubl. data).

The breeding area studied was located in the "El Curral" Intangible Reserve Zone, an area 87 ha in size, where Cinereous Harriers nested in sympatry with Long-winged Harriers (*Circus buffoni*). The area is characterized by a mosaic of shrublands consisting of the native "Curro" (*Colletia paradoxa*), the exotic blackberry (*Rubus ulmifolius*) and modified pampean grassland genera such as *Stipa*, *Bothriochloa*, *Conium*, and *Carduus* (Cabrera and Zardini 1978). Cultivated fields, pastures, tree plantations (mainly *Eucalyptus* spp.), and suburban zones surround the core study area, which is located 400 m from the closest water (Laguna de Los Padres).

Harrier pellets and prey remains were collected every 5–6 d from nesting sites, plucking stations, and roosts from September to March of 1992–93 and 1993–94. Identification of remains of birds, mammals, and amphibians found in pellets and other prey remains was based on bones, feathers, beaks, hair, and dentition. We compared these items to collections in Museo de Ciencias Naturales de La Plata, Museo de Ciencias Naturales "Lorenzo Scaglia" de Mar del Plata along with the collections of the Laboratorio de Vertebrados, Facultad de Ciencias Exactas y Naturales-Universidad Nacional de Mar del Plata. Most prey items were identified to species. During identification, pellets and prey remains in a day's collection from each breeding pair were lumped and reconstructed by matching the remiges, rectrices, beaks, and bones of birds and the fur, skull parts, and feet of mammals. This procedure minimized the possibility of overcounting the number of individuals of each species (Marti 1987).

Weights of adult birds were obtained from the literature (Fiora 1933, Contreras 1979, Salvador and Salvador 1986, Salvador 1988, 1990, Camperi 1992) and from unpublished data of the Museo de Ciencias Naturales "Lorenzo Scaglia" (Mar del Plata City). Weights of mammals were provided by M. Kittlein (unpubl. data) and V. Comparatore and A. Barbini (unpubl. data). The weight of the common toad (*Bufo arenarum*) was taken from Langone (1994). When the sex of prey could not be determined, the mean weight of males and females for that species was used. Geometric mean weights for total prey

were calculated as $\bar{x} \pm \text{SE}$ (Marti 1987). Levins' index of trophic niche breadth (Marti 1987) was calculated as follows: $B = 1/\sum_{i=1}^n p_i^2$, where p_i is the proportion of prey in different categories (mainly species). B varies from 1 to n , maximum number of prey categories. If prey are equally common in all categories, then $B = n$. If all prey belong to only one category, $B = 1$.

RESULTS

We collected 63 pellets and 45 prey remains from five Cinereous Harrier pairs breeding in 1992–93 and five pairs breeding in 1993–94. The pellets had a mean length of 35.9 ± 8.0 mm ($\pm \text{SD}$) and a mean width of 17.7 ± 2.9 mm ($N = 53$). A total of 104 prey items was identified from three taxonomic classes that included 20 vertebrate species and unidentified items (Table 1). Levins' index was 7.1 ($N = 20$). Birds accounted for 94% of the total prey items, followed by mammals (5%). Only one amphibian was identified (Table 1).

Avian prey included 14 species, with passerines being the most common of all prey (88%) (Table 1). Among passerines, House Sparrows (*Passer domesticus*) (21%), Rufous-collared Sparrows (*Zonotrichia capensis*) (19%), and Grassland Yellow-finches (*Sicalis luteola*) (19%) were the most abundant species in the diet. Doves (15%), the Eared Dove (*Zenaida auriculata*), and the Picui Ground-Dove (*Columbina picui*), were the second most numerous taxa consumed (Table 1). Among mammal prey, rodents were the most common (3%), followed by lagomorphs (2%) (Table 1). Prey weights of animals consumed ranged from 1.5 g (bird egg in one pellet) to 300 g (juvenile European hare, *Lepus capensis*) (Table 1). The geometric mean weight of prey was $31.2 \text{ g} \pm 5.5$ ($\pm \text{SE}$). Most prey (84%) weighed <60 g, and the most abundant prey were Grassland Yellow-finches, House Sparrows, and Rufous-collared Sparrows.

Birds contributed most to the total prey biomass (81%), with Eared Doves (28.2%) being the main contributor. House Sparrows (14.3%), Rufous-collared Sparrows (9.2%), and Grassland Yellow-finches (6.7%) were also important in the biomass. Biomass contributed by mammals was 15%, with juvenile European hares contributing the highest value (12.5%). Amphibian biomass was low (3.8%) in the diet of this harrier (Table 1).

DISCUSSION

Birds were the most common prey in the diet of the Cinereous Harrier, both numerically and in terms of biomass. Birds are the most common prey of many other species of *Circus* (Schipper 1973, Baker-Gabb 1981, Barnard et al. 1987, Witkowski 1989, González López 1991, del Hoyo et al. 1994, Bó et al. 1996). Cinereous Harriers preyed primarily upon passerine birds such as House Sparrows, Rufous-collared Sparrows, and Grassland Yellow-finches.

The food habits we recorded differed from those re-

Table 1. Percent total frequency of prey items, mean individual weight, and percent total biomass in the diet of Cinereous Harriers during the breeding season in southeastern Buenos Aires Province, Argentina.

PREY	% TOTAL FREQUENCY	MEAN INDIVIDUAL WEIGHT (g)	% TOTAL BIOMASS
Amphibia	(1.0) ^a		
Bufonidae			
<i>Bufo arenarum</i>	1.0 ^b	180	3.8
Birds	(94.0)		
Nonpasserine			
Columbidae			
<i>Columbina picui</i>	5.5	55	6.9
<i>Zenaida auriculata</i>	9.5	135	28.2
Picidae			
<i>Colaptes campestris</i>	1.0	200	4.2
Passerine			
Tyrannidae			
<i>Tyrannus melancholicus</i>	1.0	45	0.9
Troglodytidae			
<i>Troglodytes aedon</i>	1.0	10	0.2
Emberizidae			
<i>Sicalis luteola</i>	19.0	16	6.7
<i>Sicalis luteola</i> (egg)	1.0	1.6	<0.1
<i>Sicalis</i> spp.	2.0	16	0.7
<i>Zonotrichia capensis</i>	19.0	22	9.2
<i>Sporophila caerulea</i>	1.0	11	0.2
<i>Molothrus bonariensis</i>	2.0	62	2.6
<i>Molothrus badius</i>	2.0	53	2.2
<i>Carduelis magellanica</i>	3.0	15	0.9
<i>Carduelis chloris</i>	3.0	25	1.6
Ploceidae			
<i>Passer domesticus</i>	21.0	31	14.3
Unidentified Passeriformes	2.0	23 ^c	1.0
Unidentified birds	1.0	46 ^d	0.9
Mammals	(5.0)		
Leporidae			
<i>Lepus capensis</i> (juveniles)	2.0	300	12.5
Muridae			
<i>Oxymycterus rufus</i>	1.0	70	1.5
<i>Akodon azarae</i>	1.0	21	0.4
Unidentified murids	1.0	45 ^e	0.9
Total Number of Prey Items	104		

^a Total by prey class.
^b Total by prey species.
^c Average of the three most common passerine birds in the sample.
^d Average of all the birds in the sample.
^e Average of the two murids in the sample.

ported previously. In southernmost Chile, Jiménez and Jaksic (1988) identified a total of 1259 prey items of which 33.6% were insects, followed by birds (27.2%), mammals (19.1%), reptiles (19.1%), and arachnids (1.0%). House (in Jiménez and Jaksic 1988) also indicated that Cinereous Harriers in Chile preyed predomi-

nantly upon rats and field mice (species names not provided by these authors), and that they also ate birds, insects, and reptiles. In Tierra del Fuego, the Cinereous Harrier did not prey on birds, taking only lizards and rodents (Humphrey et al. 1970). The absence of reptiles in the diet of birds from our study area in part might

have been due to their lower availability in comparison to Chile and Patagonia.

In terms of biomass, birds were the most important group in the diet, a finding that was similar to that of Jiménez and Jaksic (1988) in southernmost Chile. Three species, Eared Dove, House Sparrow, and Rufous-collared Sparrow, made up over 52% of the biomass in our study.

When compared with the diet of Long-winged Harrier (Bó et al. 1996), which nests sympatrically with the Cinereous Harrier, we found that the values of trophic niche breadth were similar for the Long-winged Harrier (standardized Levins' index $-B' = 0.21$) and the Cinereous Harrier ($B' = 0.19$; $N = 34$). There was both overlap and divergence in the prey of these sympatric species (Pianka's overlap index = 0.67; this value calculated from data of this study and data of Bó et al. 1996). For both species, birds were the most abundant prey. For the Cinereous Harrier, birds comprised 94.2% of the diet whereas for the Long-winged Harrier, birds comprised 80%. Both harriers preyed principally upon passerines (Cinereous Harrier = 81.2%, Long-winged Harrier = 61.2%), with Rufous-collared Sparrows being most common in both diets (Cinereous Harrier = 19%, Long-winged Harrier = 27.5%). The Long-winged Harrier preyed upon aquatic birds (7.2%) which did not occur in the diet of the Cinereous Harrier. Mammals were the second most common taxa consumed by the two harriers, although the percentage varied (Cinereous Harrier = 5%, Long-winged Harrier = 17.5%). Utilization of terrestrial prey was comparable with observations of Narosky and Yzurieta (1973) who found that Cinereous Harriers were more terrestrial hunters than Long-winged Harriers.

Minimum prey weight did not vary between Cinereous Harriers (1.5 g: Grassland Yellow-finch egg) and Long-winged Harriers (1 g: insects) but the maximum weight was greater in Long-winged Harriers than that in Cinereous Harriers (Long-winged Harrier = 450 g White-faced Ibis, *Plegadis chihi*; Cinereous Harrier = 300 g juvenile European hare). However, the geometric mean weight was similar (Cinereous Harrier = 31.2 ± 5.5 g; Long-winged harrier = 32.4 ± 11.2 g).

Birds contributed most of the biomass in the diet of both species, with a higher percentage for Cinereous Harriers (81%) than for Long-winged Harriers (68%). However, the species contributing most of the biomass were not the same. Cinereous Harriers ate mainly Eared Doves and Long-winged Harriers ate mainly White-faced Ibis.

RESUMEN.—Se estudió la dieta del Gavilán Ceniciento (*Circus cinereus*) durante dos períodos reproductivos en la Reserva Integral Laguna de Los Padres, Provincia de Buenos Aires. El área de nidificación se encuentra en un ambiente arbustivo circundado por campos cultivados, pasturas, montes, lagunas y áreas suburbanas. Se recolectaron 63 egagrópilas y 45 restos presa, provenientes de

10 parejas nidificantes. Se identificaron 104 items presa, correspondiendo el 94% a las aves, el 5% a los mamíferos y un solo anfibio. La amplitud de nicho trófico (B) fue de 7.1 ($N = 20$). Los passeriformes fueron las presas más comunes (88%) del total de items presa, dentro de las cuales el Gorrión (*Passer domesticus*), el Chingolo (*Zonotrichia capensis*) y el Misto (*Sicalis luteola*) fueron las principales especies capturadas. La media geométrica del peso de presas consumidas fue de $31.2 \text{ g} \pm 5.5$ ($\bar{x} \pm \text{SE}$) (rango = 1.5–300 g). En cuanto a la biomasa aportada las aves contribuyeron en un 81%. La dieta del Gavilán Ceniciento en la provincia de Buenos Aires difirió con otras áreas de estudio (Chile y zona Patagónica) pero presentó similitud con su congénere el Gavilán Planeador (*Circus buffoni*) nidificando en simpatria.

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ABUNDANCE OF THE OGASAWARA BUZZARD ON CHICHIJIMA, THE PACIFIC OCEAN

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KEY WORDS: *Ogasawara buzzard*; *Buteo buteo toyoshimai*; Bonin; endemic; density.

The Ogasawara buzzard (*Buteo buteo toyoshimai*) is an insular subspecies of the Common Buzzard (*B. buteo*, Ornithological Society of Japan 1974, Brazil 1991, Monroe and Sibley 1993). It is endemic to the Ogasawara (Bonin) Islands, which lie about 1000 km south of Tokyo in the Pacific Ocean. It usually nests on rocky cliffs (Funatsu and Chiba 1991), although tree nesting has been recently reported (Takagi and Ueda 1998, Kato and Suzuki 1999). It differs from a nearest subspecies, *B. buteo japonicus*, because of its drab plumage with less brown on the uppers

and its longer beak and shorter wings and tarsi (Momi-yama 1927).

The Ogasawara buzzard is listed as an endangered species in Japan (Japan Environmental Agency 1998) because the population is so small. It is known to inhabit the two island groups of the Ogasawaras, Chichijima-retto, and Hahajima-retto (Brazil 1991), with total areas of 38.2 km² and 27.0 km², respectively (Ogasawara Natural Environmental Group 1992). Among the islands, Chichijima is the largest and probably supports the largest population of buzzards. It is also the most developed of the Ogasawara Islands with a human population of about 1900 in 1998. In the early 1990s, the number of pairs of Ogasawara buzzards on Chichijima was estimated to be

about 15 (Higuchi et al. 1988, Funatsu and Chiba 1991) but no recent estimates of the present population have been made. Here, we present the results of a study we undertook to estimate the number of pairs currently on Chichijima.

STUDY AREA

Chichijima is situated at 27°04'N and 142°13'E and is approximately 24 km² in area. Terrain on the island is steep with many mountain areas of volcanic origin but elevations do not exceed 326 m. There are many rocky coastal and mountain cliffs that provide potential nest sites for Ogasawara buzzards. Chichijima is generally covered with low vegetation and canopy trees consisting of native and introduced species do not exceed 15 m in height (Shimizu and Tabata 1991). About 73% of Chichijima is covered with regenerated native forests and scrubs, and the remaining 27% includes coastal forests, exotic low shrubs (*Leucaena leucocephala*) and grasses (*Stachytarpheta jamaicensis*), cultivated fields, crags, and village areas.

METHODS

We systematically searched Chichijima for Ogasawara buzzards in March, April, May, June, August, and December 1998 and February, March, April, and May 1999 (1–2 wk per mo) during which time at least one of us stayed on Chichijima. When buzzards were found, we recorded their numbers, spatial position, flight path, any social interactions, and other patterns of behavior. Whenever possible, buzzards were individually identified using plumage characteristics, plumage deficits or differing stages of plumage development. When necessary, we searched presumed territories to determine occupancy. In so doing, we considered two nonantagonistic adults inhabiting a putative territory to be a pair.

RESULTS AND DISCUSSION

We found a total of 28 territorial pairs and one unmated, territorial individual by March 1999 and reconfirmed their occupancy of territories in May 1999. The pairs were dispersed rather evenly in both native and introduced habitats. For 16 of the 28 pairs, breeding activity was confirmed either by observing deliveries of nesting materials to nests, adults attending nests, incubating adults, nestlings in nests, or fledglings in their territories. For the remaining eight pairs, neither attended nests nor fledglings were found; nevertheless, we suspected that they bred because we observed them either delivering prey to presumed nests, repeatedly visiting and leaving the same locations (probably nesting sites) on cliffs, or they showed aggressive or alert behavior when we entered their territories during the breeding season.

Our estimate of 28 pairs of Ogasawara buzzards on Chichijima was nearly twice that previously reported for the island (Suzuki 1982, Higuchi et al. 1988, Funatsu and Chiba 1991). However, a comparison of our data with previous reports indicated that the increase was mainly due to the fact that we surveyed the island more thor-

oughly. Therefore, it is unlikely that the population of buzzards on the island has increased in recent decades.

We estimated the density of the buzzard population on Chichijima to be approximately 1.2 pairs per km². Our density estimate was rather high compared to densities of other breeding populations of Common Buzzards. Densities up to 0.78 pairs per km² have been reported in wooded areas of middle Europe (Newton et al. 1982) but normally densities are <0.5 pairs per km² (Newton 1979, Newton et al. 1982, Dare and Barry 1990, Davis and Davis 1992, Halley 1993, Jedrejewski et al. 1994, Penteriani and Faivre 1997). Factors limiting raptor population are food supply, nest-site availability, and human intrusion (Newton 1991). No other raptors, excluding occasional visitors, inhabit Chichijima; therefore, the high density of Ogasawara buzzards on Chichijima may be due to the abundance of nest sites and the lack of competition from other raptors for food. It may also be due to the overall absence of human persecution.

The density of buzzards also appears to be high on other islands in Chichijima-retto and Hahajima-retto, although recent survey data are not available (Higuchi et al. 1988, Funatsu and Chiba 1991, Suzuki 1991). We estimated the total population of Ogasawara buzzards on the Ogasawara Islands to be only about 85 pairs using our density estimate of 1.2 pairs per km² on Ogasawara and a total area of potential habitat of 70.7 km² including Mukojima-retto, the third island group of the Ogasawaras. Further study is needed to better document the total population of Ogasawara buzzards, including nonterritorial individuals, and to determine its nesting ecology to insure the future conservation of the subspecies.

RESUMEN.—*Buteo buteo toyoshimai* es endémico a las Islas Ogasawara (Bonin), a 1000 km al sur de Japón. Investigamos el número de parejas de *Buteo buteo toyoshimai* en Chichijima (ca. 24 km²), la isla más grande de las Ogasawara, en 1998–99. Veintiocho parejas fueron encontradas. Este estimativo fue el doble que el previamente reportado, probablemente debido a la búsqueda minuciosa hecha en la isla. La densidad de parejas (1.2 parejas por km²) fue más alta en comparación con los valores de *Buteo buteo* reportados en otras partes del mundo.

[Traducción de César Márquez]

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LETTERS

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GOLDEN EAGLE ATTACKS AND KILLS ADULT MALE COYOTE

Golden Eagles (*Aquila chrysaetos*) attack and kill a wide range of small mammals, birds, and reptiles (e.g., Olendorff 1976, *Am. Midl. Nat.* 95:231–236; Johns 1977, *Blue Jay* 35:92–93; Servheen 1978, *Murrelet* 59:77; O’Gara 1994, Pages E41–E48 in S.E. Hygnstrom, R.M. Timm, and G.E. Larson (Eds.), *Prevention and Control of Wildlife Damage*. USDA, Animal and Plant Health Inspection Service, Animal Damage Control, Washington, DC U.S.A.). When the abundance of preferred prey declines (Steenhof and Kochert 1988, *J. Anim. Ecol.* 57:37–48), Golden Eagles will attack larger animals, including sheep and cattle (Arnold, 1954, USFWS Cir. 27; Lock and Stephen 1959, *J. Anim. Ecol.* 28:43–50; Bergo 1987, *Fauna Norv. Ser. C. Cinculus* 10:95–102; Phillips et al. 1996, *Wildl. Soc. Bull.* 24:468–470), reindeer (*Rangifer tarandus*; Nybakk et al. 2000, *Wildl. Soc. Bull.* 27:1038–1042), ibex (*Capra ibex*; Nievergelt 1966, *Der alpensteinbock Capra ibex L. in seinem Lebensraum* Verlag Paul Parey, Hamburg, Germany), red deer (*Cervus elaphus*; Northeast 1978, *Br Birds* 71:36–37; Rebecca 1986, *Scott. Birds* 14:86), pronghorn (*Antilocapra americana*; Deblinger and Alldredge 1996, *J. Raptor Res.* 30:157–159), and roe deer (*Capreolus capreolus*; von Raesfeld 1965, *Das rehwild*, Verlag Paul Parey, Hamburg, Germany). Apparently, such depredation on large mammals is neither unusual nor site specific (Nybakk et al. 2000). Golden Eagles also will attack other predators, including Peregrine Falcons (*Falco peregrinus*; VanZandt 1982, *Colo. Field Ornithol.* 16:20–21) and red fox (*Vulpes vulpes*; Hatch 1968, *Blue Jay* 26:78–80). Eagles have been seen feeding on coyote (*Canis latrans*; e.g., Woelfl and Woelfl 1994, *Can. Field-Nat.* 108:494–495) carcasses, but no incidents of actual killing of coyotes have been reported.

On 23 December 1998 at 1600 H, I observed a coyote running along the crest of a hill in sagebrush-grass steppe 20 km northeast of Preston, ID U.S.A. A Golden Eagle circling perhaps 20 m above the hill stooped on the coyote and struck it just behind the shoulders knocking it to the ground. Almost immediately (within 10 sec), the eagle released the coyote and the coyote stood and ran over the crest of the hill. After a few moments (perhaps 30 sec), the eagle flew off in the direction the coyote disappeared. I arrived at the attack site about 20 min. later and followed the coyote’s tracks and a blood trail in fresh snow. I flushed the eagle from a coulee about 50 m from the top of the hill and found the coyote where the eagle was. The coyote was dead and the body cavity had been opened just below the ribs. The heart and portions of the liver were missing. The stomach and intestines remained intact, although they had been pulled from the carcass.

The coyote was an adult male and the carcass (minus the portion consumed by the eagle) weighed 13.5 kg. There were two sets of puncture wounds just anterior to the shoulders. Each set consisted of two punctures about 4 cm apart with a third wound about 10 cm behind. This pattern is typical of an eagle attack (Wade and Browns 1984, *Texas Agric. Ext. Serv. Publ. No. B-1429*). I skinned the coyote and found that the talons had punctured the lungs and aorta. There were no other obvious wounds.

Others have reported eagle attacks on coyotes and eagles feeding on coyote carcasses. Woelfl and Woelfl (1994) reported four Golden Eagles feeding on a freshly killed coyote pup in southeastern Alberta, Canada. They surmised that the coyote was surprised and killed while foraging about 300 m from cover. Ford and Alcorn (1964, *Condor* 66: 76–77) and Dekker (1985, *Can. Field-Nat.* 99:383–385) described several unsuccessful Golden Eagle attacks on coyotes. Bowen (1980, *J. Mammal.* 61:376–377) and Wells and Bekoff (1978, *J. Mammal.* 59:886–887) reported apparent competition among Bald Eagles (*Haliaeetus leucocephalus*), Golden Eagles, and coyotes for carrion. All reports of eagle predation on coyotes describe attacks during winter and early spring (Woelfl and Woelfl 1994).

Golden Eagles will attack a variety of large mammals, most frequently during winter and early spring, times of the year when food is scarce or nutritional requirements may be high (e.g., Deblinger and Alldredge 1996; Seguin and Thibault 1996, *Rev. Ecol. Terre Vie* 51:329–339). The available evidence suggests that these attacks are generally successful, provided that the quarry can be individually isolated (Nybakk et al. 2000), and that it can be ridden until it collapses from exhaustion, shock, or internal injuries (Watson 1997, *The Golden Eagle*, T. & A.D. Poyser, London, U.K.).

While limited, there is literature suggesting that mammalian predators are more likely to attack large prey when provisioning offspring (Till and Knowlton 1983, *J. Wildl. Manage.* 47:1018–1025; Knowlton et al. 1999, *J. Range Manage.*, 52:398–412). I speculate that the same motivation could, in part, explain predation by Golden Eagles on relatively large animals. During the nesting season, Golden Eagles will kill 230 kg domestic calves (O’Gara 1978, *Proc. Vertebr*

Pest Conf. 8:206–213; Grahm 1986, *Scott. Birds* 14:86; Phillips and Blom 1988, *Proc. Vertebr. Pest Conf.* 13:241–244; Phillips et al. 1996), adult domestic sheep and lambs (Svendson 1980 *Var Fuglefauna* 3:20–26 Hewson 1984, *J. Appl. Ecol.* 21: 843–868; Scrivner et al. 1990, Univ. Calif. Hopland Field Stn. Publ. No. 101:10–13) and adult reindeer (Nybak et al. 2000). Although large prey are most often selected in inverse relationship to the availability of smaller prey (e.g., Steenhof and Kochert 1988), killing of livestock can occur even when small otherwise preferred prey such as jackrabbits (*Lepus* spp.) and ground squirrels (*Spermophilus* spp.) are readily available (Phillips et al. 1996). Likewise, Nybak et al. (2000) documented winter and early spring predation on semidomesticated reindeer calves and does. Halda (1983, *Fauna* 36:101) reported late winter and early spring Golden Eagle predation on mature roe deer. Tigner (1973, *Southwest. Nat.* 18:346–348), Goodwin (1977, *Auk* 94:789–790) and Deblinger and Alldredge (1996) all reported eagle attacks on adult and fawn pronghorns in spring. Northeast (1978) and Rebecca (1986) reported winter and spring attacks on red deer; Lawson and Johnson (1982, Pages 1037–1055 in J.A. Chapman and J.A. Feldhammer [Eds.], *Wild mammals in North America: biology, management and conservation*, Johns Hopkins Univ. Press, Baltimore, MD U.S.A.) reported predation on bighorn sheep lambs (*Ovis canadensis*) and Wigal and Coggins (1982, Pages 1008–1020 in J.A. Chapman and J.A. Feldhammer [Eds.], *Wild mammals in North America: biology, management and conservation*, Johns Hopkins Univ. Press, Baltimore, MD U.S.A.) reported killing of mountain goat (*Oreamnos americanus*) kids.

Seasonal differences in prey selection by eagles, especially as they might reflect changes in nutritional requirements, have not been well investigated (Seguin and Thibault 1996) and the available evidence is somewhat contradictory. Some studies, for example, suggest that large prey are favored early in nesting (Fernandez and Ceballos 1990, *Ornis Scand.* 21:236–238). Others suggest that such prey are unimportant for nesting birds but instead are favored by overwintering eagles (Mollhagen et al. 1976, *J. Wildl. Manage.* 36:784–792). Because there are data consistent with the possibility that prey-size selection by mammalian predators may be influenced by the number of offspring being fed (Till and Knowlton 1983), it might be worthwhile to investigate whether there is evidence of a similar facultative response expressed by raptors.

I thank M. Fall, A. Harmata, and C. McIntyre for comments on the manuscript.—**J.R. Mason, USDA, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, Utah State University, Logan, Utah 84322-5295 U.S.A.**

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GOLDEN EAGLE PAIR KILLS FERRUGINOUS HAWK IN WYOMING

We saw a pair of Golden Eagles (*Aquila chrysaetos*) kill a lone adult Ferruginous Hawk (*Buteo regalis*) in Thunder Basin National Grassland (TBNG) in East Central Wyoming on 20 June 1999. The attack took place around 1100 H in the Rochelle Hills area (43°52'18"N, 105°01'42"W). We were sitting in a stopped vehicle and watched the attack from 0.8 km away. The eagles alternatively dove upon the hawk as it flew less than 7 m from the ground. The attack lasted about 25 min from the time we first observed it and consisted of five dives by each eagle. The attack sequence entailed one eagle diving on the hawk followed within 30 sec by the second when the hawk was occupied with the first eagle. The Ferruginous Hawk either rolled onto its back exposing its talons to the diving eagles or turned sharply to avoid contact. On the fifth attempt, the second eagle hit the hawk in the air. The eagle continued to hold onto the dead hawk as they fell to the ground where the eagle mantled the hawk. Previous literature indicated this tandem hunting strategy used by eagles taking black-tailed jackrabbits (*Lepus californicus*) and a red fox (*Vulpes fulva*) in which one eagle either flushed the prey or diverted its attention while the second eagle attacked (Hatch 1968, *Blue Jay* 26: 78–80, Collopy 1983, *Auk* 100:747–749). We did not determine the sex of the eagle that made the kill. The second eagle landed 2 m away and both eagles remained on the ground for 5 min. Neither eagle consumed any of the carcass and the pair flew off together. We watched the event from a distance and did not harass the eagles forcing them to abandon the kill. Neither eagle appeared disturbed for any reason but remained calm during the time spent on the ground and as it flew away.

Golden Eagles prey upon a variety of species ranging in size from small rodents to ungulates such as antelope (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) (Hogstrom and Wiss 1992, *Ornis Fenn.* 69:39–44, Watson et al. 1993, *Ibis* 135:387–393, Deblinger and Alldredge 1996, *J. Raptor Res.* 30:157–159). Golden Eagles have attacked

other birds of prey for a variety of reasons including food robbing, predation, and nest defense (Hays 1987, *J. Raptor Res.* 21:87–5, Ferrer 1990, *J. Raptor Res.* 24:210–218; Clouet et al. 1999, *J. Raptor Res.* 33:102–109). In TBNG, Golden Eagles and Ferruginous Hawks often pursue similar prey species, primarily the black-tailed prairie dog (*Cynomys ludovicianus*) and several lagomorphs. We wondered if the eagles might be defending a food source from a potential competing species but it did not seem likely.

Nest defense was examined as a possible explanation for the attack. A search of the area did not reveal any nest but it may have been overlooked due to irregular terrain. Even though a nest was not located, nest defense seemed be the logical explanation for this attack. Protection of nestlings may have been the reason for the attack even though Ferruginous Hawks have not been known to take Golden Eagle nestlings. Golden Eagles do aggressively defend their nesting territory from other raptor species (Watson 1997, *The Golden Eagle*, T. & A.D. Poyser, London, U.K.). The Golden Eagle pair may have been protecting its nest from a perceived threat.—**Matt L. Buhler, Jake H. Powell, and Stanley H. Anderson, Wyoming Cooperative Fish and Wildlife Research Unit, P.O. Box 3166, University of Wyoming, Laramie, WY 82071 U.S.A.**

BOOK REVIEW

EDITED BY JEFFREY S. MARKS

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Handbook of the Birds of the World, Volume 5. Barn-owls to Hummingbirds. Edited by Josep del Hoyo, Andrew Elliott, and Jordi Sargatal. 1999. Lynx Edicions, Barcelona, Spain. 759 pp., 76 color plates, 406 color photographs, 758 distribution maps, 3 figures, and 1 table. ISBN 84-87334-25-3. Cloth, \$185.00.—The *Handbook of the Birds of the World* (HBW) will be the first series to illustrate all of the species of birds on earth and to provide access to all of the essential information about each one of them. In fact, the editors claim that it will be the first work to deal with each member of an entire class of the animal kingdom. HBW is not yet half completed—it will consist of 12 volumes in all—and yet it already totals 3519 pages in volumes 1 to 5. The rate of production has been impressive considering the immense volume of material contained and that the first volume appeared in 1992.

Volume 5, reviewed here, completes coverage of the raptors begun with the falconiforms in Volume 2. In addition to the Strigiformes, Volume 5 covers Caprimulgiformes and Apodiformes, but the majority of this review will be concerned with the owl sections considering the primary interests of the readership of the *Journal of Raptor Research*.

The owl portion of Volume 5 was written by 13 authors, including some well-recognized owl experts and some individuals who will not be familiar even to those who follow the owl literature closely. More surprising than the use of little-known authors is that many living owl experts are not among the authors of this work.

A Forward discusses factors concerning risks to survival of bird populations in general and is followed by a very brief Introduction that notes three new developments for Volume 5: more plates and photographs, the longest single-species account to date (the Barn Owl [*Tyto alba*]), and the inclusion of details on restricted-range species.

Illustration of the species covered in this volume could only be described as lavish: the photographs

and paintings are excellent. Nineteen artists contributed the 76 color plates, seven of whom produced the owl plates. My only complaint regarding the color plates is that the heads of the tytonids are uniformly too large in proportion to their bodies. Outstanding photographs show species in natural habits illustrating a variety of behaviors.

The bulk of the book is taken up with family and species accounts: two families for the strigiforms (242 pages), five for the caprimulgiforms (144 pages), and three for the apodiforms (294 pages). Each family account begins with a map of the group's worldwide distribution, the general distinguishing characteristics, size range, habitat requirements, the number of genera and species, the number of species considered to be threatened, and the number that are extinct. Family accounts range from 6 to 77 pages in length and are followed by accounts for each species. Species accounts range in length considerably, reflecting the extent of knowledge on the various species.

Tytonidae, containing only 16 species, is the third longest family account in the book, mirroring the wide geographic range and quantity of information available on the group. M.D. Bruce compiled a huge quantity of knowledge about the biology of tytonids, but I noted a few discrepancies between what Bruce presented and the original sources. For example, in the second paragraph on page 57, P.A. Stewart used 30°N latitude in the United States to delimit northern and southern populations of Barn Owls for the purpose of studying dispersal. Bruce, however, gives 3°N as the latitudinal demarcation. In the first paragraph on page 54, Bruce's summary of the results of my study on lifetime reproductive success in Barn Owls incorrectly states that in one year, 11% of owl pairs produced second broods. This should have read that over the 19-year study, 11% of pairs produced double broods. The latitudinal error may be typographical, and the second-brood error may be the result of a too-hasty reading of only the paper's abstract. They render some doubt, however, about the accuracy of other information in the account.

The family account of Strigidae is about twice as long as that of Tytonidae for a family with 12 times the number of species. A good discussion of recent DNA-DNA hybridization and mitochondrial DNA data reaffirms that strigiforms and falconiforms are not closely related despite their host of shared adaptations for prey capture. DNA also clearly confirms that the caprimulgiforms are the closest relatives of strigiforms. Just like the account of Tytonidae, this account presents a huge quantity of information on the biology of the typical owls.

One of the most serious criticisms of previous volumes of HBW (Gill, *Condor* 96:566–567, 1994; Jehl, *Condor* 100:405–409, 1998; Bates, *Condor* 100:

769–775, 1998; Brightsmith, *Auk* 116:1158–1159, 1999) was that literature citations are not given in the text, making it difficult or impossible to ascertain the source of a particular bit of information. I, too, found this omission to be a frustration, making the large body of references included less useful than it could have been.

The entire HBW series with its extensive access to the literature and wonderful illustrations is a must for every library, but the cost and sheer bulk may deter individual ornithologists from obtaining the entire set. Raptor biologists, though, will want to add volumes 2 and 5 to their libraries.—**Carl D. Marti, Raptor Research Center, Boise State University, Boise, ID 83725 U.S.A.**

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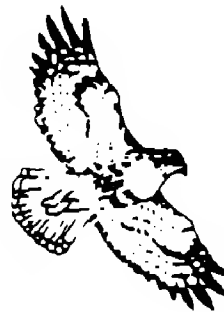


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2000 ANNUAL MEETING

The Raptor Research Foundation, Inc. 2000 annual meeting will be held on 8–11 November in Jonesboro, Arkansas, U.S.A. For information about the meeting contact James C. Bednarz, Department of Biological Sciences, Arkansas State University, P.O. Box 599, State University, AR 72467 U.S.A. Telephone 501-972-3082, E-mail jbednarz@navajo.astate.edu.

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The **Fran and Frederick Hamerstrom Award** recognizes an individual who has contributed significantly to the understanding of raptor ecology and natural history. Contact: **Dr. David E. Andersen, Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108 U.S.A.** Deadline: August 15.

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The **James R. Koplin Travel Award** is given to a student who is the senior author of the paper to be presented at the meeting for which travel funds are requested. Contact: **Patricia A. Hall, 5937 E. Abbey Road, Flagstaff, AZ 86004 U.S.A.**

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Grants²

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